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Integration of Major QTLs of Important Agronomic Traits in Soybean

Guohua Hu, Qingshan Chen, Chunyan Liu,
Hongwei Jiang, Jialin Wang and Zhaoming Qi

*Northeast Agricultural University,
Land Reclamation Research & Breeding Centre of Heilongjiang
P. R. China*

1. Introduction

Soybean [*Glycine max* (L.) Merr.] is one of the most important crops in the world, accounting for 48% of the world market in oil crops, and is used mostly for animal feed and for oil production. In soybean, most agronomic traits, such as abiotic stress, biological stress, protein concentration, oil content and yield, are quantitative traits controlled by multiple genes. Moreover, genotypic expression of the phenotype is environmentally dependent, which affected QTLs detection greatly. QTLs detection was also affected by marker sets, experimental design, mapping populations, and statistical methods, which result in the location of QTLs mapped by the same marker differently.

From the first publication of quantitative trait locus (QTL) of soybean using molecular markers (Paterson et al. 1988), numerous QTLs underlying different traits of soybean have been identified in different genetic backgrounds and environments. However, few identical QTLs were identified in same experimental population or same environment by different researchers or in different years (Orf 1999; Mansur 1993, 1996). All of these interfered in QTLs to improve oil content of soybean by marker-assisted selection (MAS). Integrated QTL analysis can facilitate the identification of “real” QTL and has attracted a great deal of attention.

Recently, the International Maize and Wheat Improvement Center put forward a proposal to find universal QTLs by building a consensus map. This proposal offers a basis for QTL analysis and marker-assisted selection (MAS). Meta-analysis method led to about twofold increase in precision in the estimates of QTL position compared to the most precise initial QTL position within the corresponding region.

In this chapter, QTL meta-analysis for major agronomic traits in soybean was performed for the first time. Published QTLs were collected, a consensus map of published maps with a reference map was created, consensus QTLs were acquired by the meta-analysis approach, genes were mined using bioinformatics tools, and markers of consensus QTLs with high effects and small CIs were provided for MAS.

2. Collection of important agronomic traits QTLs

2.1 Collection of seed quality QTLs

2.1.1 Oil content QTLs

Oil and protein concentration account for about 60% of dry soybeans by weight, protein at 40% and oil at 20%. The 130 QTLs for soybean oil content published in the last 20 years were

No. of QTL	Parent 1	Parent 2	Population Size	Analysis Method	Population type	Reference
11	Charleston	Dong nong594	154	CIM MIM	RIL	Shan,2008
10	Zhong Dou 29	Zhong Dou 32	255	CIM	RIL	Wang,2008
4	Charleston	Dong nong594	154	CIM	RIL	Chen,2007
2	01-042 (G.max)	KT-156(G.soja)	120	CIM	F ₂	Zhang,2008
1	Wan 82-178	Tong Shan Bo Pi	133	CIM	RIL	Xu,2007
3	He Feng 25	Xin Min 6	122	CIM	RIL	Ly,2006
2	Ke Xin 3	Zhong Huang 20	192	CIM	F ₄	Zhu,2006
2	Sui Nong 14	Sui Nong 20	94	CIM	F ₂	Zhu,2006
4	Jin 23	Hui Bu-Zhi	474	CIM	RIL	Liang,2005
3	N87-984-16	TN93-99	101	ANOVA	RIL	Panthee,2005
3	BSR 101	LG82-8379	167	ANOVA	RIL	Kabelka,2004
6	Essex	Williams	131	CIM	RIL	Hyten,2004
4	Wan 82-178	Tong Shan Bo Pi	133	CIM	RIL	Li,2004
4	Charleston	Dong nong594	154	CIM	RIL	Zhang ZC,2004
3	Zheng 92116	Shang 951099	105	IM	F _{2,3}	Yang,2004
1	Ke Feng 1	Nan Nong1138-2	184	CIM	RIL	Zhang WK,2004
1	A3733	PI437088A	76	ANOVA	RIL	Chung,2003
3	Ke Feng 1	Nan Nong1138-2	201	CIM	RIL	Wang,2001
2	Ke Feng 1	Nan Nong1138-2	201	IM	RIL	Wu,2001
3	Ma.Belle	Proto	82	ANOVA	F ₂	Csanadi,2001
5	Minsoy	Noir 1	236	ANOVA	RIL	Specht,2001
1	A81-356022	PI468916	98	IM	BC ₃ F ₄	Sebolt,2000
1	Parker	PI468916	100	IM	BC ₃ F ₄	Sebolt,2000
2	Archer	Minsoy	233	IM	RIL	Orf,1999
3	Archer	Noir 1	240	IM	RIL	Orf,1999
1	Essex	Peking	200	ANOVA	F _{2,3}	Orf,1999
1	Minsoy	Noir 1	240	IM	RIL	Orf,1999

1	M82-806	HHP	71	ANOVA	F _{2.5}	Brummer,1997
1	M84-49	Sturdy	92	ANOVA	F _{2.5}	Brummer,1997
3	A87-29601	CX1039-99	100	ANOVA	F _{2.5}	Brummer,1997
3	C1763	CX1159-49	89	ANOVA	F _{2.5}	Brummer,1997
3	C1763	CX1039-99	83	ANOVA	F _{2.5}	Brummer,1997
1	M81-382	PI 423.949	81	ANOVA	F _{2.5}	Brummer,1997
5	PI97100	Coker237	111	ANOVA	F ₂	Lee,1996
6	Young	PI416937	120	ANOVA	F ₄	Lee,1996
5	Minsoy	Noir 1	284	ANOVA	RIL	Mansur,1996
2	Minsoy	Noir 1	284	IM	RIL	Mansur,1993
9	A81-356022	PI 468916	60	ANOVA	F _{2.3}	Diers,1992
5	Misuzudaizu	Moshidou Gong 503	-	ANOVA IM	-	Tajuddin,2003
Total:130						

Table 1. Information of oil content QTLs

collected from Soybase and 28 published articles (Table 1). Mansur (1996) mapped five oil QTLs of soybean by the population Minsoy and Noir 1 with the ANOVA method. Sebolt (2000) mapped a oil QTLs of soybean by the population A81-356022 and PI 468916 with the Interval Mapping (IM) method. Hyten (2004) mapped six oil QTLs of soybean by the population Essex and Williams with the Composite Interval Mapping (CIM) method. Shan (2008) first reported the interaction between QTLs and environments with RIL population, crossed by Charleston and Dongnong594, with CIM and Multiple Interval Mapping(MIM) method.

The population used for above research involved RIL, F₂, F₄, F_{2.3}, F_{2.5}, and BC₃F₄. Information on interval mapping (IM), composite interval mapping (CIM), multiple interval mapping (MIM), and the ANOVA analysis method was obtained. 1 to 11 QTLs were mapped from different papers.

2.1.2 Protein concentration QTLs

In the former researches, QTLs come from the 18 papers and soybase website listed in Table 2. Diers (1992) mapped eight protein QTLs of soybean by the population A81-356022 and PI 468916 with the ANVOA method. Furthermore, Diers (2000) reanalyzed and mapped a protein QTLs of soybean by the population A81-356022 and PI 468916 with the IM method, so the new QTLs were used in this study. In several cases, the same populations had been used by different research in independent experiments. For the Minsoy × Noir 1 population, Mansur (1996) mapped three protein QTLs of soybean with the ANVOA method, Orf (1999) mapped two protein QTLs of soybean with the IM method, Specht (2001) mapped five protein QTLs of soybean with the ANVOA method. For the Charleston × Dongnong 594 population, QTL × Environment effects were developed (Shan Dapeng et al., 2009), and used to reanalyze the new phenotypic data (Chen Qingshan et al., 2007; Zhang Zhongchen et al., 2004).

The set of 107 seed protein concentration QTL (Table 2) was obtained from 21 populations, varying in size from 60 to 284. The analytical methods used to predict the QTL included ANOVA and both simple and composite interval mapping. The population type included RILs, F₂, F_{2.3}, F₄, F_{2.5}, and BC₃F₄. A few QTLs with a LOD score below 2.0 were discarded from the analysis to reduce the risk of including false positives.

QTL Number	Parent1	Parent2	Population Size	Analysis Method	Population Type	Reference
10	Charleston	Dongnong 594	154	CIM	RIL	Shan,2009
5	Charleston	Dongnong 594	154	CIM	RIL	Chen,2007
2	Charleston	Dongnong 594	154	CIM	RIL	Zhang,2004
3	Zheng 92116	Shang 951099	105	IM	F _{2:3}	Yang,2004
3	Kefeng 1	Nannong 1138-2	201	IM	RIL	Wu,2001
1	A3733	PI437088A	76	ANOVA	RIL	Chung,2003
1	A81-356022	PI468916	98	IM	BC ₃ F ₄	Sebolt,2000
1	Parker	PI468916	100	IM	BC ₃ F ₄	Sebolt,2000
1	M82-806	HHP	71	ANOVA	F _{2:5}	Brummer,1997
1	M84-49	Sturdy	92	ANOVA	F _{2:5}	Brummer,1997
2	McCall	PI 445.815	92	ANOVA	F _{2:5}	Brummer,1997
2	A87-29601	CX1039-99	100	ANOVA	F _{2:5}	Brummer,1997
3	C1763	CX1159-49	89	ANOVA	F _{2:5}	Brummer,1997
2	C1763	CX1039-99	83	ANOVA	F _{2:5}	Brummer,1997
1	LN83-2356	PI 360.843	69	ANOVA	F _{2:5}	Brummer,1997
2	Archer	Minsoy	233	IM	RIL	Orf,1999
1	Archer	Noir 1	240	IM	RIL	Orf,1999
2	Minsoy	Noir 1	240	IM	RIL	Orf,1999
10	BSR 101	LG82-8379	167	ANOVA	RIL	Kabelka,2004
6	PI97100	Coker237	111	ANOVA	F ₂	Lee,1996
13	Young	PI416937	120	ANOVA	F ₄	Lee,1996
6	Essex	Williams	131	CIM	RIL	Hyten,2004
2	Essex	Peking	200	ANOVA	F _{2:3}	Qiu,1999
4	Ma.Belle	Proto	82	ANOVA	F ₂	Csanadi,2001
6	Misuzudaizu	Moshidou Gong 503	-	ANOVA , IM	-	Tajuddin,2003
1	N87-984-16	TN93-99	101	ANOVA	RIL	Panthee,2005
5	Minsoy	Noir 1	236	ANOVA	RIL	Specht,2001
3	Minsoy	Noir 1	284	ANOVA	RIL	Mansur,1996
8	A81-356022	PI 468916	60	ANOVA	F _{2:3}	Diers,1992
Total :	107					

Table 2. The origin of the set of seed protein concentration QTL included in the meta-analysis (The table details the number of QTL mapped in each population, along with the identity of the parents, the size and the type of each population)

2.1.3 Fatty acid QTLs

83 QTLs come from the 8 papers and soybase website were listed in Table 3. Among them, 16 QTLs were related with palmitic acid content; 11 QTLs related with stearic acid content; 32 QTLs related with oleic acid content; 10 QTLs related with linoleic acid content; and 14

QTLs related with linolenic acid content. In 2007, Lee summerized 60 QTLs related with fatty acid from 2002 to 2008. Some RFLP markers, not appear in the soybean public genetic map, were discarded. The analytical methods used to predict the QTL included ANOVA, IM, CIM, and MIM. The population type included RILs, F₂, F_{2:3}, F₄, RIL, and BC₁F₁.

Trait	Marker	LG	Population Type	Data analysis	Reference
Palmitic acid	Satt537	D1b	RIL	CIM	Panthee,2006
Palmitic acid	Satt330-Sat_155	I	BC ₁ F ₁	CIM MIM	Zheng, 2005
Palmitic acid	Satt175	M	F ₂	ANOVA	Li,2002
Palmitic acid	Sat_132	O	RIL	CIM ANVOA	Yarmilla,2006
Palmitic acid	Satt684	A1	F ₄	SAS	Andrea,2007
Stearic acid	Sat_245-Satt373	L	BC ₁ F ₁	CIM MIM	Zheng, 2005
Stearic acid	Satt249	J	RIL	CIM	Panthee,2006
Stearic acid	Satt474	B2	F ₂	BSA	Spencer,2004
Stearic acid	Sat_090	F	RIL	CIM & ANVOA	Yarmilla,2006
Oleic acid	Satt143	L	F _{2:3}	CIM	Maria,2008
Oleic acid	Sat_356-Satt615	D2	BC ₁ F ₁	CIM & MIM	Zheng, 2005
Oleic acid	Satt263	E	RIL	CIM	Panthee,2006a
Oleic acid	Satt163	G	RIL	CIM ANVOA	Yarmilla,2006
Linoleic acid	Satt349	K	RIL	CIM & ANVOA	Yarmilla,2006
Linoleic acid	Satt166-Satt156	L	BC ₁ F ₁	CIM & MIM	Zheng, 2005
Linoleic acid	Satt235	G	RIL	CIM	Panthee,2006
Linoleic acid	Sat_274	O	RIL	IM	Masayuki,2008
Linolenic acid	Satt579-Satt600	D1b	BC ₁ F ₁	CIM & MIM	Zheng, 2005
Linolenic acid	Satt185	E	RIL	CIM	Panthee,2006
Linolenic acid	Satt349	K	RIL	CIM & ANVOA	Yarmilla,2007

Table 3. Reported information of fatty acid QTLs in soybean

2.1.4 Amino acid content QTLs

For the QTL information of amino acid content, only 3 researches involved (Panthee, 2006b, 2006c; Bingchang Zhuang, 2000). In total, 111 QTLs were mapped with RIL population.

2.1.5 Isoflavone content QTLs

The reseach of isoflavone content was very few. 70 QTLs were mapped in 3 papers (Kassem, 2004; Meksem, 2001a; Guoliang Zeng, 2007) by RIL population.

2.2 Collection of biotic stress resistance QTLs

2.2.1 Fungal disease resistance QTLs

Diseases caused by fungal pathogens account for approximately 50% of all soybean disease losses around the world. Conflicting results of fungal disease resistance QTLs from different populations often occurred. 107 QTLs in recent years of fungal disease resistance content were collected from 23 papers (Table 4). Only 1 to 5 QTLs were obtained in most researches. These QTLs had been mapped on the soybean linkage groups (LGs). not all fungal disease resistance content QTLs were collected because of some QTLs could not be projected to the reference map.

QTL number	Population-type	Name of fungal disease	Reference
5	F ₂	Soybean rust	Alexandre, 2008
2	RIL	Brown stem rot	Bachman, 2001
8	RIL	Phytophthora root rot	Burnham, 2003
3	RIL	Phytophthora root rot	Weng, 2007
2	RIL	Asian soybean rust	Danielle, 2008
5	RIL	Sclerotinia stem rot, White mold	Guo, 2008
1	NIL	Soybean rust	Hyten, 2007
5	RIL	Sudden death syndrome	Kazi, 2008
2	RIL	Asian soybean rust	Monteros, 2007
1	F ₂	Frogeye leaf spot	Mian, 1999
34	RIL	Sclerotinia stem rot, White mold	Arahana, 2001
1	RIL	Frogeye leaf spot	Zhang, 2004
3	RIL	Sudden death syndrome	Njiti, 2002
10	RIL	Brown stem rot	Patzoldt, 2005a
6	RIL	Rhizoctonia root and Hypocotyl rot	Zhao, 2005
5	F ₂	Sudden death syndrome	Austeclinio, 2007
2	RIL	Phytophthora root rot	Han, 2008
2	RIL	Brown stem rot	Lewers, 1999
1	NIL	Brown stem rot	Patzoldt, 2005b
4	RIL	Sudden death syndrome	Iqbal, 2001
2	NIL	Sudden death syndrome	Meksem, 1999
1	RIL	Sudden death syndrome	Bell-Johnson, 1999
2	F ₂	Phomopsis seed decay	Berger, 1999
Total: 107			

Table 4. QTLs information of fungal disease resistance in soybean

2.2.2 Insect resistance QTLs

81 QTLs from the 15 papers and soybase website were listed in Table 5. Among them, 12 QTLs were related with soybean aphid resistance, 42 QTLs related with corn ear worm(CEW) resistance, 11 QTLs related with common cut worm(CCW) resistance, and 16 QTL related with Mexican bean beetle and soybean pod borer resistance. The average interval of all above QTLs were 15 cM. The analytical methods used to predict the major site included BSA, ANOVA, IM, CIM, and MIM. The population type included RILs, F₂, F_{2:3}, F_{3:4}, RIL, and BC₆ population.

Name of insect-resistance	QTL number	Population-type	Analysis Method	Reference
Soybean aphid	2	F _{2:3}	BSA	Li,2007
Soybean aphid	2	F ₂ , F _{2:3}	BSA	Mian,2008
Soybean aphid	8	F _{3:4}	CIM, MIM, ANOVA	Zhang,2009
CCW	2	F ₂	CIM	Kunihiko,2005
CCW	2	RIL	CIM	Liu,2005
CCW	3	RIL	CIM	Fu,2007
CCW	4	F ₂	CIM	Kunihiko,2007
CEW	2	F _{2:3}	IM	Rector,2000
CEW	2	F ₂	ANOVA, IM	Rector,1998
CEW	10	RIL	SAS, IM	Terry, 1999
CEW	20	RIL	IM	Terry, 2000
CEW	5	F _{2:3}	IM	Narvel, 2001
CEW, SBL	3	BC ₆ F _{2:3}	ANOVA	Zhu, 2006
Mexican bean beetle	1	F _{2:3}	ANOVA	Boerma, 2005
Soybean pod borer	15	RIL	CIM	Zhao, 2008
Total	81			

Note: CIM, composite interval mapping; BSA, bulk segregant analysis; IM, Interval mapping; ANOVA, Analysis of variance; CCW, common cut worm; CEW, corn ear worm; SBL, Soybean looper

Table 5. QTLs information of insect-resistance in soybean

2.2.3 Soybean cyst nematode resistance QTLs

Soybean cyst nematode is a very serous disease, reducing yields by as much as 75 percent. Many research was focus on the major QTL mapping. 135 QTLs underlying SCN No.1, 2, 3, 4, 5, 6, and 14 resistance from 23 papers and soybase website were listed in Table 6. For different research, 1 to 19 QTLs were analyzed. The analytical methods included GLM, BSA, ANOVA, IM, and CIM. The population type included RILs, F₂, F_{2:3}, F₄, RIL, NIL, and BC.

2.3 Collection of yield trait QTLs

2.3.1 100-Seed weight QTLs

Soybean seed size is determined by the genetics of the variety and the environment where the seed was produced. In America, seed size was described as seeds per pound, but in China, seed size was often defined as 100-seed weight. So the research of QTL mapping for 100-seed weight was mainly in China. Among them, the population crossed by Kefeng 1 and Nannong 1138-2 were used for 3 times. The analytical methods included IM and CIM. The population type included RILs and F₂. In total, 78 QTLs were collected(Table 5).

QTL number	Population-type	Analysis method	References
10	F _{2:3}	CIM	Guo, 2006a
17	F ₂	GLM	Kabelka, 2005
4	F ₄	CIM	Glover, 2004
1	RIL	GLM	Prabhu, 1999
9	F _{2:3}	CIM	Guo, 2006b
7	F _{2:3}	GLM	Yue, 2001a
4	BC ₃ F _{2:3} , F _{2:3}	IM	Schuster, 2001
19	F _{2:3}	GLM	Yue, 2001b
11	BC ₁ F ₂ , BC ₁ F ₄	CIM,MIM	Lu weiguo, 2005
1	F ₂	BSA	Wang hui, 2007
3	RIL	BSA	Li Yongchun, 2007
1	RIL, NIL	ANOVA	Meksem, 2001b
4	F ₂	BSA & CIM	Meng Xi, 2008
12	F ₂ , BC ₁ F ₂	CIM	Wang, 2001
1	F _{2:3}	Stepwise regression	Vierling, 1996
3	RIL	CIM	Ferdous , 2006
6	F _{2:3}	ANOVA	Qiu, 1999
1	NIL	ANOVA	Meksem, 1999
9	F _{2:3}	GLM	Brucker, 2005
3	F _{2:3}	GLM	Concibido, 1994
1	Population	GLM	Mahalingam, 1995
5	F _{2:3}	GLM	Heer, 1998
3	F _{2:3} , RIL	ANOVA	Concibido, 1996
Total	135		

Table 6. QTLs reported on resistance to soybean cyst nematode

No. of QTLs	Parents	Population Size	Analysis methods	Population type	Reference
3	Kefeng 1×Nannong 1138-2	201	CIM	RIL	Gai,2007
1	Kefeng 1×Nannong 1138-2	184	CIM	RIL	Zhang,2004
6	Kefeng 1×Nannong 1138-2	201	IM	RIL	Wu,2001
3	Zheng 92116×Shang 951099	105	IM	F ₂	Guan,2004
11	G.max'7499'×G.soja PI 245331	148	CIM	BIL	Li,2008
8	Charleston×Dongnong 594	154	CIM	RIL	Chen,2007
2	Jindou 23×Huibuzhiheidou	-	CIM	RIL	Wang,2004
28	Zhongdou 29×Zhongdou 32	255	CIM	RIL	Wang,2008
3	Suinong 14×Suinong20	94	CIM	F ₂	Zhu, 2006
Total	65				

Table 7. Information of 100-Seed Weight QTLs

2.3.2 Lodging QTLs

Soybean (*Glycine max* [L.] Merr.) grain yields may be reduced when the plants lodge, So soybean lodging characteristics are an important consideration when conditions favor high yields. Lodging also creates harvesting problems. Where higher yields are obtained under irrigation, lodging is a major factor to consider in variety selection, water management, and planting density. 59 QTLs from 16 papers and soybase website were listed in Table 8. For different research, 1 to 8 QTLs were obtained. Most research only got only 1 to 2 QTLs. The analytical methods included IM, CIM, ANOVA, SSMD, and MNTECRLO. The population type included RILs and F₂, F₅, and BC₂F₄.

No. of QTLs	Parents	Population size	Analysis Methods	Population type	Reference
4	Kefeng 1×Nannong 1138-2	184	CIM	RIL	Huang,2008
6	Zhongdou 29×Zhongdou32	165	CIM	RIL	Zhou,2009
6	Jindou 23 ×Huibuzhiheidou	257	SSMD	RIL	Wang,2004
7	Pis×Beeson/ kenwood/ Lawrence	236	CIM	RIL	Guzman,2007
1	<i>G. max</i> × <i>G. soja</i>	120	CIM	RIL	Li,2008
4	Essex × Forrest	100	CIM	RIL	Li,2008
1	Kefeng 1×Nannong 1138-2	206	CIM	RIL	Zhang,2004
1	Essex × Forrest	100	CIM	RIL	Kassem,2006
1	<i>G. max</i> IA2008× <i>G. soja</i> PI468916	468	CIM	BC ₂ F ₄	Wang,2003
8	PI416937 × Young	120	ANOVA	F ₄	Lee,1996
5	Minsoy × Noir 1	240	IM	RIL	Orf,1999
2	Archer × Minsoy	233	IM	RIL	Orf,1999
5	Minsoy × Noir 1	236	ANOVA	RIL	Chase,2001
1	---	177	ANOVA	F _{4:6}	Chase,2001
2	Noir 1 × Minsoy	284	ANOVA	RIL	Mansur,1996
1	BSR 101 × LG82-8379	167	ANOVA	F ₅	Kabelka, 2004
1	IA2008 × PI 468916	468	MNTECRLO	BC ₂ F ₄	Wang,2003
2	Coker237 × PI97100	111	ANOVA	F ₂	Lee,1996
1	---	248	BSA	RIL	Mansur,1993
Total	59				

Table 8. Information of lodging QTLs in soybean

2.3.3 Plant height QTLs

Plant height become one of important agronomic traits with the increase of planting density. Many factors affect the height of a soybean plant, but the genetic loci is the most important, and the rapid developments of molecular markers have provided powerful tools to map the height-related QTL at the genomic level. 93 QTLs from 13 papers and soybase website were

listed in Table 9. For different research, 1 to 19 QTLs were obtained. The analytical methods were mainly IM and CIM. The population type included RILs and F₂.

No. Of QTLs	Parents	Population size	Analysis methods	Population type	Reference
5	Zheng92116×Shang951099	105	IM	F ₂	Guan,2004
4	Kefeng1×Nannong1138-2	201	IM	RIL	Wu,2001
19	Zhongdou29×Zhongdou32	255	CIM	RIL	Wang,2008
5	Suinong14×Suinong20	94	CIM	F ₂	Zhu,2006
8	Kefeng1×Nannong1138-2	184	CIM	F ₂	Zhang,2004
1	G. max '7499' × G. soja PI 245331	295	CIM	RIL	Li,2008
6	G. max IA2008×PI 468916	468	CIM	RIL	Wang,2004
1	Minsoy × Noir 1	-	IM	RIL	Mansur,1993
11	BSR 101× LG82-8379	167	-	RIL	Kabelka,2004
2	Essex ×Williams	-	-	RIL	Chapman,2003
8	Jindou23 ×Huibuzhiheidou	-	CIM	RIL	Wang Z,2004
8	Charleston×Dongnong594	154	CIM	RIL	Chen,2007
15	Charleston×Dongnong594	147	CIM & MIM	RIL	Sun,2010
Total	93				

Table 9. Information of soybean height QTLs

2.4 Soybean growth stages QTLs

Soybean growth stages divides plant development into vegetative (V) and reproductive (R) stages. The vegetative stages are numbered according to how many fully-developed trifoliolate leaves are present. The reproductive (R) stages begin at flowering and include pod development, seed development, and plant maturation. 98 QTLs from 10 papers and soybase website were listed in Table 10. For different research, 1 to 44 QTLs were obtained. The analytical methods were Multiple-QTL model, CIM, IECM, ANOVA, SIM, and Chi-square. The population type included F₂, RIL and BC₂.

QTL-number	Population type	Analysis method	References
1	F ₂	Multiple-QTL model	Naoki,2001
13	F ₂	CIM	Wang Zhen,2004
3	NIL	IECM	Wang Ying,2008
14	RIL	ANOVA	Green,2001
10	RIL	SIM	Adler,1999
3	RIL	ANOVA	Funastuki,2005
5	RIL	Chi-square	Chase,2001
3	BC ₂	CIM	Diers,2004
2	F ₂	ANOVA	Mansur,1996
44	RIL	CIM	Dawei Xin,2007
Total	98		

Table 10. QTLs published of soybean growth stages

3. QTL projection and integration: a consensus map of soybean important agronomic traits

3.1 QTL projection of seed quality traits
3.1.1 Oil content QTLs projection on a consensus map

In total, 110 QTLs for oil content were projected onto the reference map soymap2, and a consensus map was generated. The projected QTLs covered all LGs of the reference map (Fig. 1). Some QTLs could not be projected onto the reference map because they had no common markers with the reference map. As Fig. 1 shows, each LG contained many QTL clusters, and at least two original QTLs were found in each QTL cluster. On LG A1, 7 independent QTLs from different research were projected on the same interval.

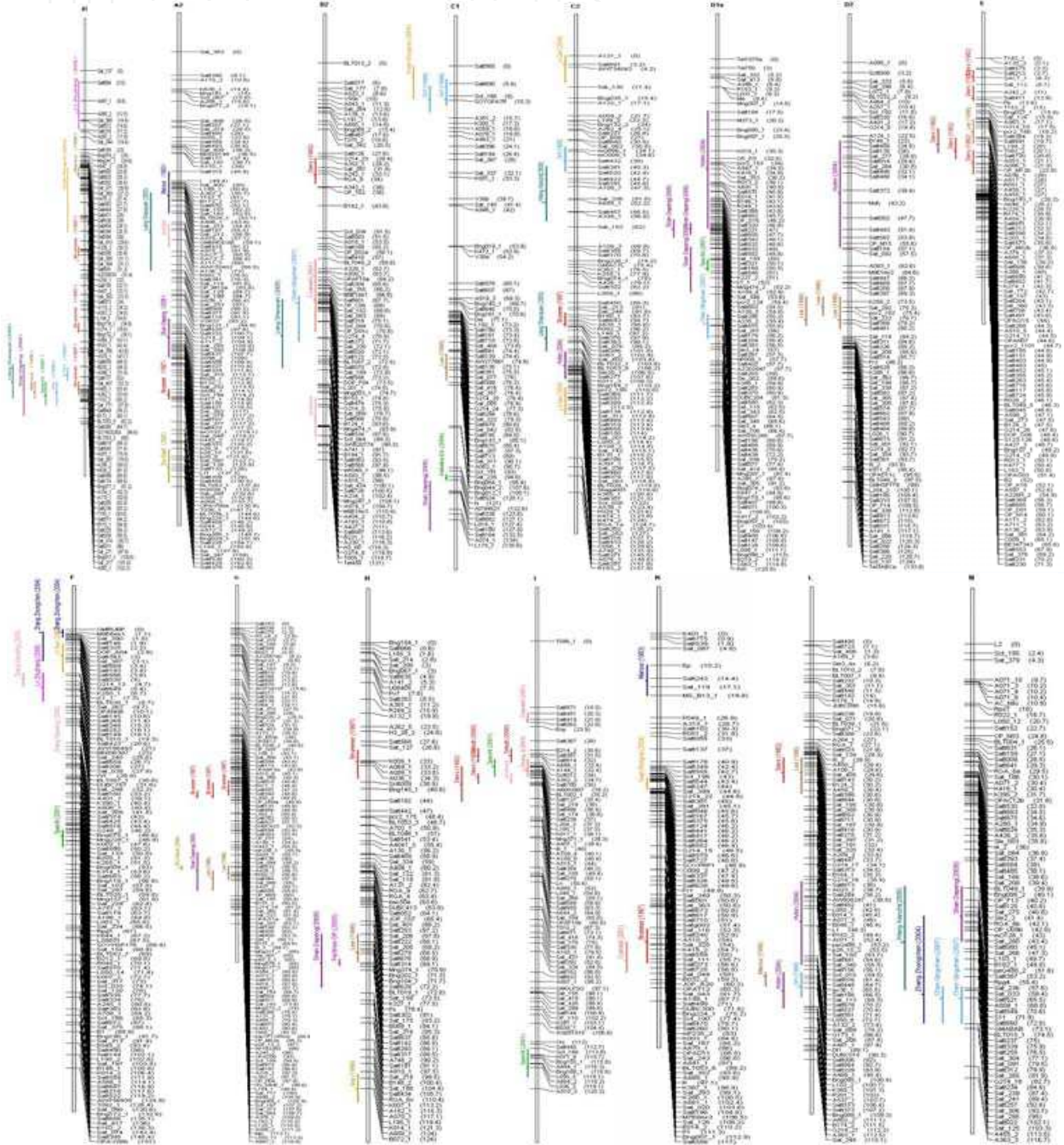


Fig. 1. Consensus map of soybean oil content

3.1.2 Protein concentration QTLs projection on a consensus map

In total, 70 QTLs of 23 clusters identified, Fig. 2 illustrates the QTL clusters identified: there appear to be one very common site on chromosomes I, at this site, nine QTL was predicted from the various populations to be present. Four metaQTL sites, one each on chromosomes A1, B2, E, and M, at each of these sites, at least four QTL were predicted from the various populations to be present. Eighteen metaQTL site, one each on chromosomes A2, B1, B2, C1, C2, E, G, H, N and O. At each of these sites, at least two QTL were predicted from the various populations; the CIs of these clustered QTL shared a 3cM overlap with one another.

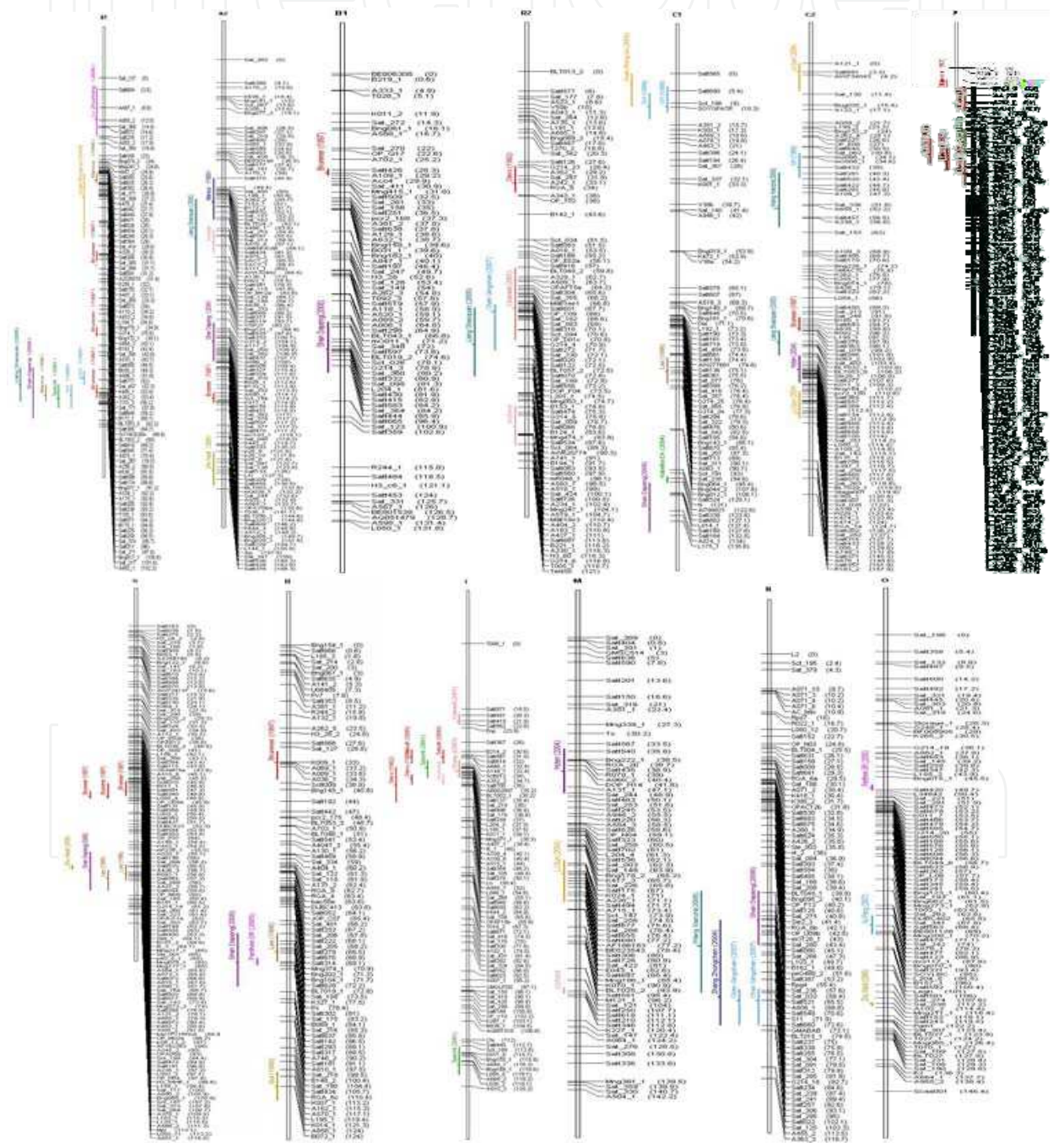


Fig. 2. Consensus map of soybean protein concentration

3.1.3 Fatty acid content QTLs projection on a consensus map

Different genetic map with their QTLs were projected on the soybean public map Soymap2 to construct a consensus map of major QTLs for fatty acid content in soybean. The consensus QTLs distributed in clusters on A1, B2, D1b, D2, E, G, and L linkage groups (Fig.3).

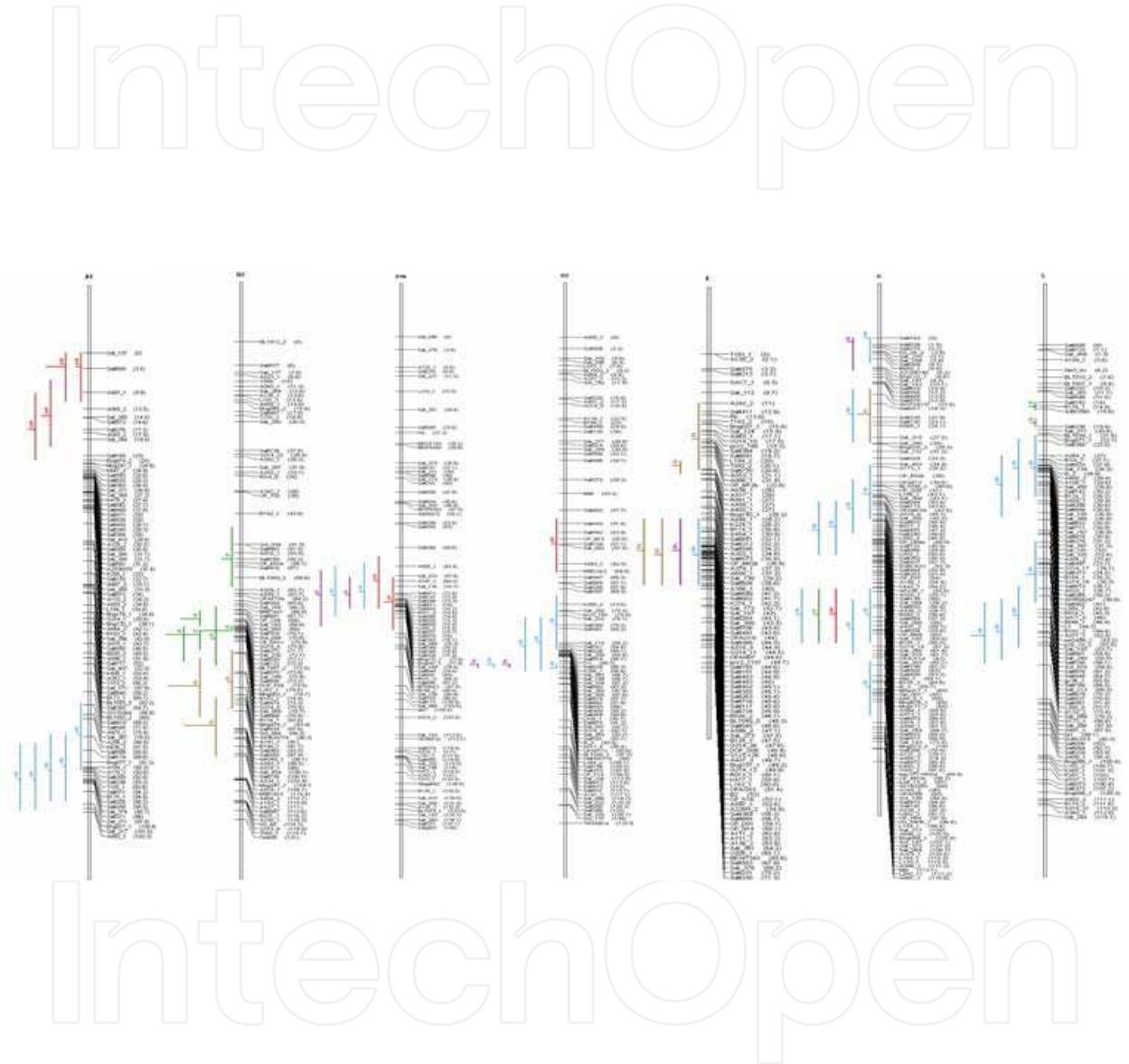


Fig. 3. Consensus map of fatty acid QTLs in soybean

3.1.4 Amino acid content QTLs projection on a consensus map

For amino acid content in soybean, 26 consensus QTLs for different amino acid on 16 linkage groups, that is A1, A2, B2, C1, D1a, D1b, D2, E, F, G, I, J, K, L, M, and O, were constructed (Fig.4). However, each consensus QTL included not only one kind but a few different kind of amino acids, which would be a key to explain that the same locus could influence the content of many kind of amino acids.

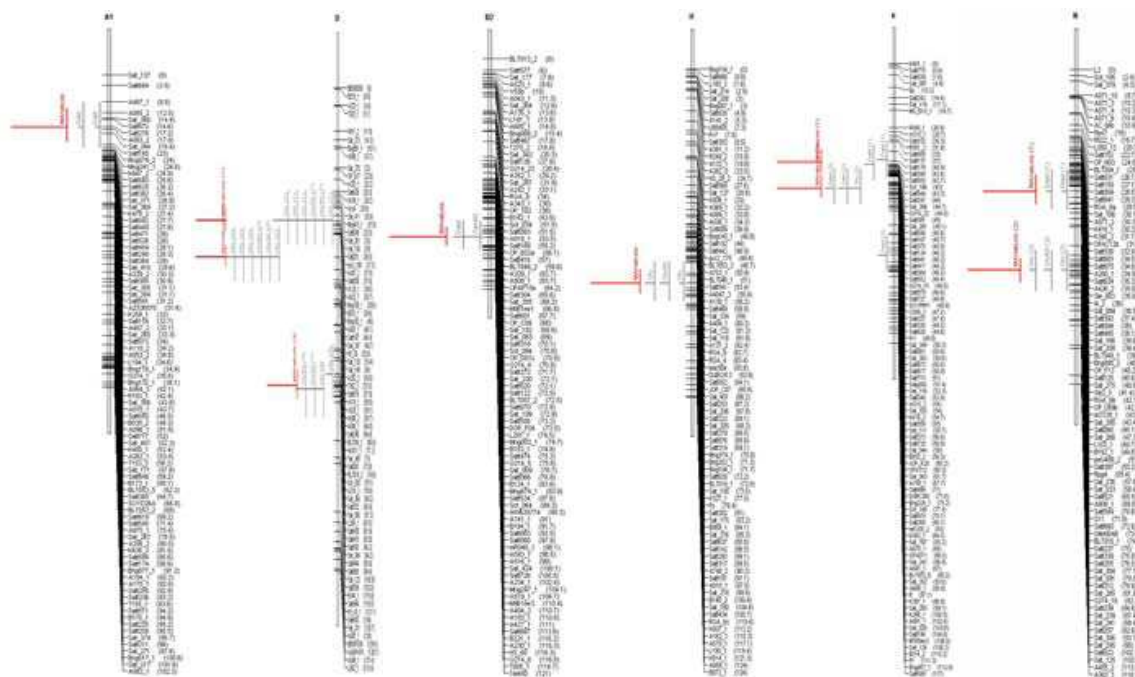


Fig. 5. Isoflavone content QTLs projection on a consensus map

3.2 QTL projection of biotic stress resistance traits

3.2.1 Fungal disease resistance QTLs projection on a consensus map

QTLs of original map were projected on the reference map by map-projection function of BioMercator2.1. In total, 107 QTLs of fungal disease resistance were projected on the reference map, soymap2, and a consensus map was obtained (Fig. 6).

As the Fig. 6 shown, projected QTLs were covered 11 linkage groups of the reference map. Although these original QTLs were mapped in different genetic backgrounds and with different methods, they were projected on the same regions by the common marker. If a QTL cluster contained more than two QTLs from different researches, this region could contain a potential allele in a high probability.

3.2.2 Insect-resistance QTLs projection on a consensus map

81 QTLs of original map were projected on the reference map. For single insect-resistance trait, the consensus QTLs mainly focused on 4 linkage groups, E, F, H, and M (Fig. 7). The cluster on linkage group E was obviously in a narrow interval. In detail, 3 consensus QTLs were distributed on linkage group F and M for soybean aphid-resistance. 9 consensus QTLs were discovered on 6 linkage group D1a, D2, E, G, H, and M for Corn Earworm. No consensus QTLs were found for Common Cutworm. For multiple insect-resistance trait, 14 consensus QTLs were combined on 8 linkage group D1a, D2, E, F, G, H, M, and N (Fig. not shown).

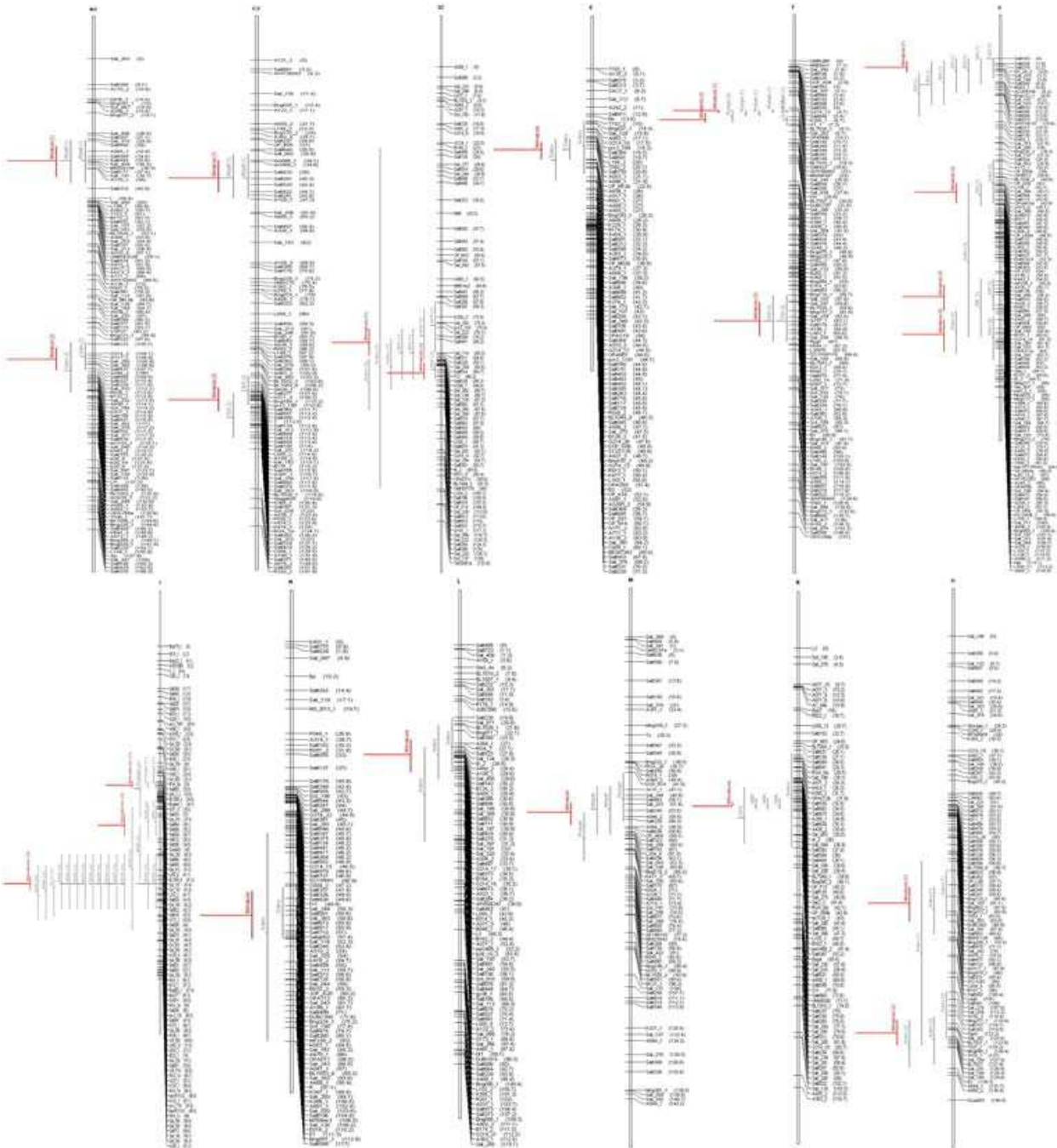


Fig. 6. QTLs of original map projection. BSR (Brown stem rot) ; Phytoph (Phytophthora root rot) ; ASR (Asian soybean rust) ; Sclero (Sclerotinia stem rot, White mold) ; SBR (Soybean rust) ; SDS (Sudden death syndrome) ; FLS (Frogeye leaf spot) ; RR-HR (Rhizoctonia root and Hypocotyl rot) ; PSD (Phomopsis seed decay)

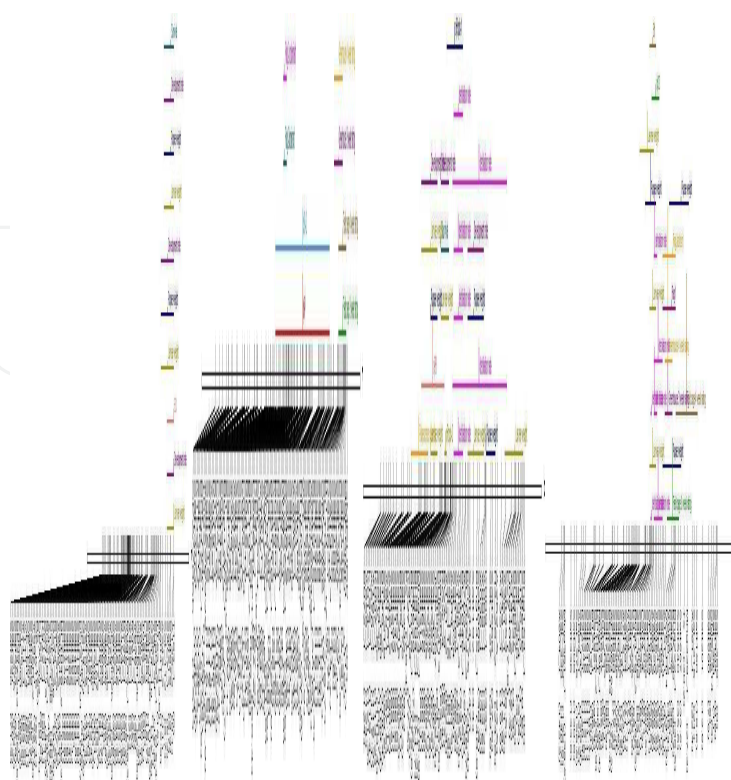


Fig. 7. Consensus map of insect-resistance QTLs in soybean

3.2.3 Soybean cyst nematode resistance QTLs projection on a consensus map

151 QTLs of original map were projected on the reference map (Fig. 8). 16 consensus QTLs on 8 linkage groups A2, B1, B2, D2, E, G, H, and J were integrated. In detail, 3 consensus QTLs were distributed on linkage group B1, B2, and G for SCN Race 1-resistance. 1 consensus QTLs were distributed on linkage group B1 for SCN Race 2-resistance. 7 consensus QTLs were distributed on linkage group A2, E, G, and J for SCN Race 3-resistance. 3 consensus QTLs were distributed on linkage group A2, G, and H for SCN Race 4-resistance. 1 consensus QTLs were distributed on linkage group B1 for SCN Race 5-resistance. 1 consensus QTLs were distributed on linkage group D2 for SCN Race 14-resistance.

3.3 QTL projection of yield traits

3.3.1 100 seed weight QTLs projection on a consensus map

65 QTLs of original map were projected on the reference map (Fig. 9). 10 consensus QTLs on 9 linkage groups B1, C2, D2, K, M, and O were integrated for additive effect. 4 consensus QTLs on 3 linkage groups B2, H, and I were clustered for reductive effect.

3.3.2 Lodging QTLs projection on a consensus map

59 QTLs of original map were projected on the reference map (Fig. 10). 11 consensus QTLs were distributed on 5 linkage group, B1, C2, F, G, and L. Only one consensus cluster were found on linkage group B1 and G, but 2 on linkage group C2 and F, and 5 on linkage group L.

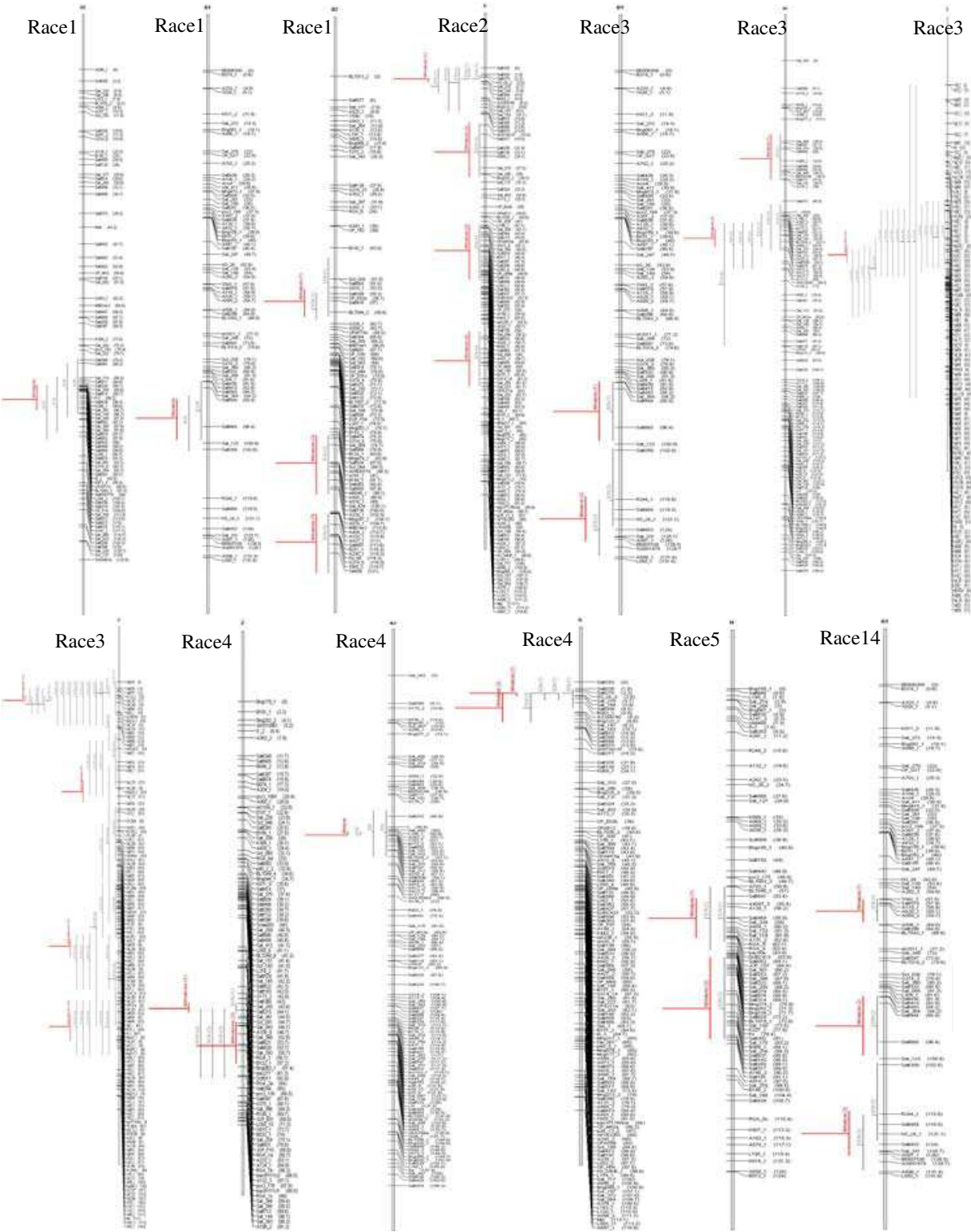


Fig. 8. Consensus map of QTLs resistant to SCN

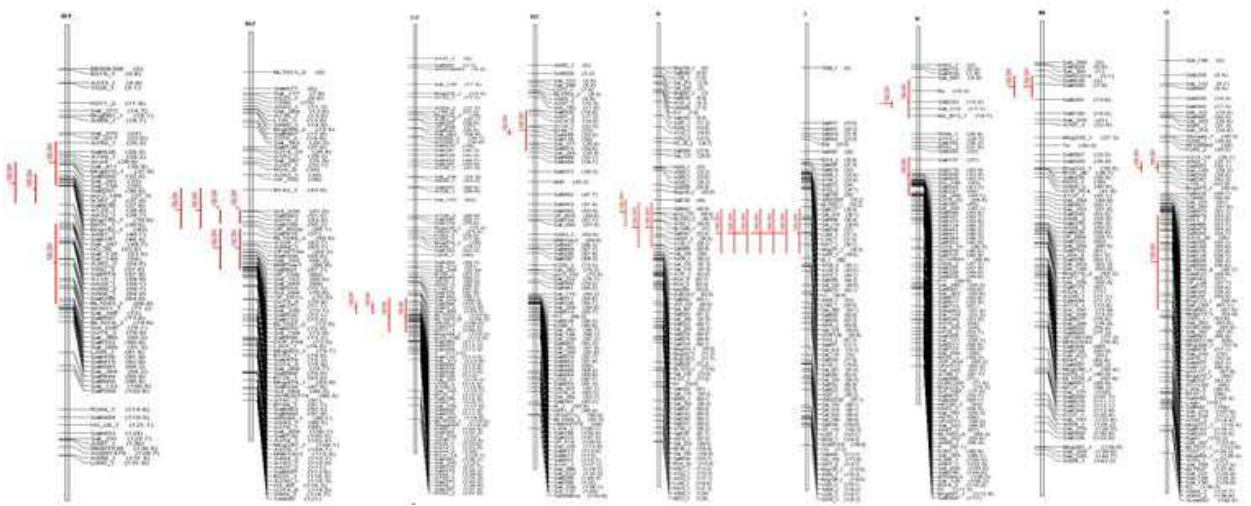


Fig. 9. Consensus map of 100 seed weight in soybean

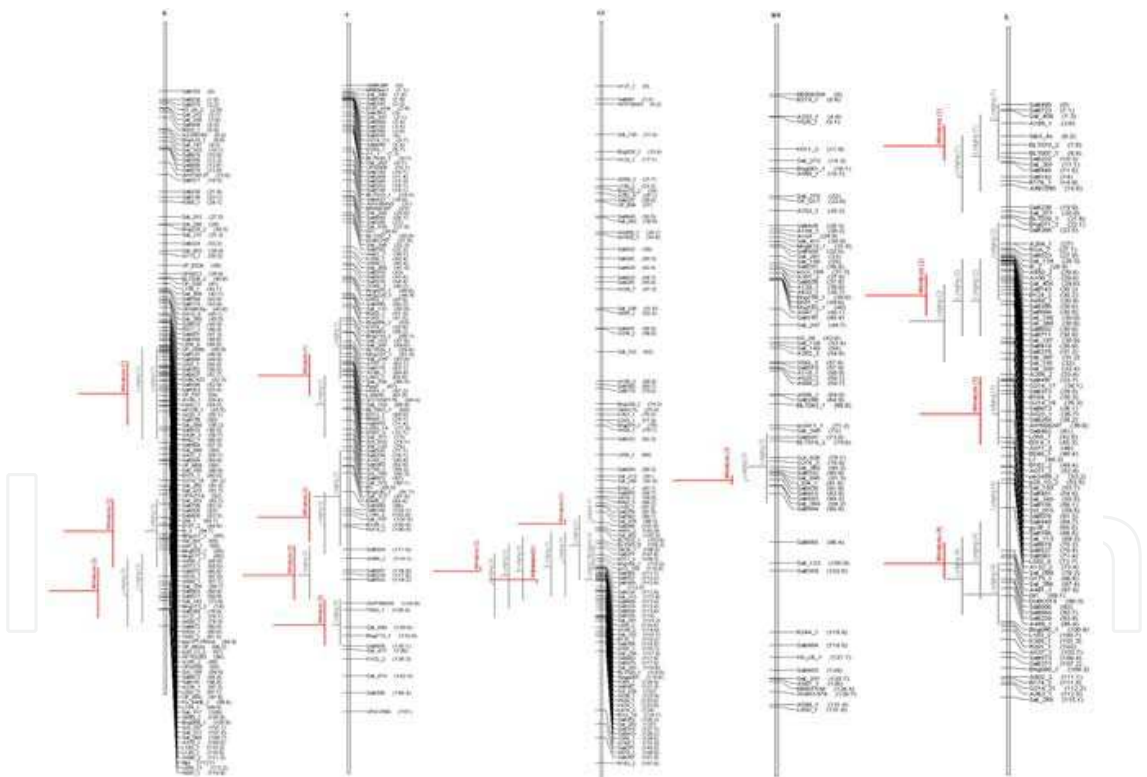


Fig. 10. Consensus map of Lodging QTLs

3.3.3 Plant height QTLs projection on a consensus map

78 QTLs of original map were projected on the reference map(Fig. 11). 12 consensus QTLs were distributed on 7 linkage group, B1, C2, D1a, F, G, K, and M.

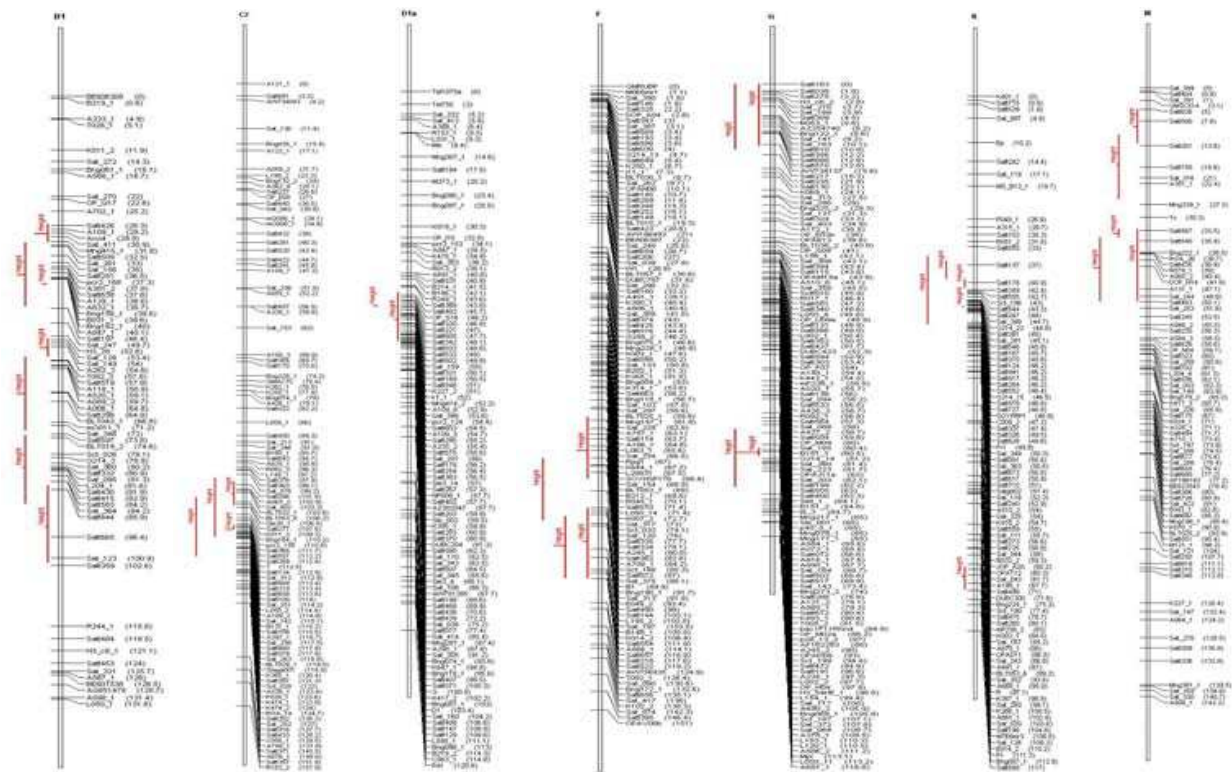


Fig. 11. Height QTLs projection on a consensus map

3.4 Soybean growth stage QTLs projection on a consensus map

98 QTLs of original map were projected on the reference map (Fig. 12). 7 consensus QTLs were distributed on 3 linkage group C2, L, and M for R1 period. 2 consensus QTLs were distributed on 2 linkage group C2 and L for R8 period. 10 consensus QTLs were distributed on 5 linkage group C1, D1a, D1b, F, and J for mixed periods(Fig. not all shown).

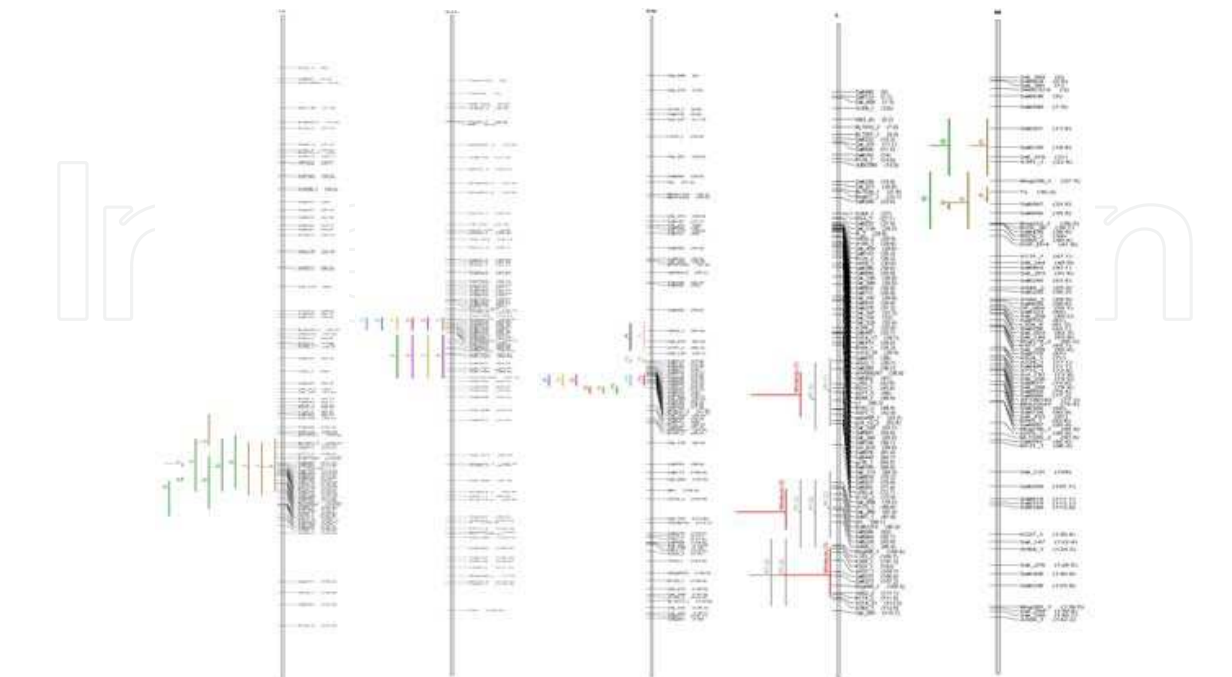


Fig. 12. Consensus map of soybean growth stage

4. Meta-analysis for important agronomic traits

4.1 Meta-analysis results of seed quality QTLs

4.1.1 Meta-analysis of Oil content QTLs

A meta-analysis was carried out on the consensus QTL sites on 25 QTL clusters (Table 11). The site on linkage group A1 merged five QTL, with flanking markers at 92.56cM and 94.20cM, a C.I. of 1.49cM and an R² value of 10.83%. The site on linkage group I merged five QTL into a single consensus QTL. The flanking markers for this site lay at 36.03cM and 49.30cM, the CI of the QTL was 12.35cM, and its R² value was 18.22%. The site on linkage group G merged four QTL into a single consensus QTL. The flanking markers for this site lay at 94.40cM and 96.60cM, the CI of the QTL was 1.71cM, and its R² value was 13.27%. The confidence interval at all sites ranged from 1.49-12.35cM. The mean R² values ranged from 5.5% to 39.15%.

LG	AIC value	Meta-QTL position(cM)	95% C.I. (cM)	Map distance	Original QTL number	Mean R ²	L-marker	L-marker Position (cM)	R-marker	R-marker Position (cM)
A1	48.99	93.5	92.75-94.24	1.49	5	10.83	A170_1	92.56	Satt511	94.20
A1	48.99	29.19	28.18-30.21	2.03	2	29.18	Satt454	28.08	A329_2	30.28
A1	48.99	88.24	86.91-89.57	2.66	2	38.41	Satt599	85.58	Bng077_1	91.24
A2	18.01	70.96	66.97-74.95	7.98	2	39.15	A111_1	67.328	Satt341	77.695
B2	53.37	72.83	69.15-76.51	7.36	3	9.56	Sat_083	68.98	Sat_009	78.66
C1	54.37	10.43	7.68-13.19	5.51	3	8.67	Satt690	5.36	A351_2	15.70
C1	54.37	123.94	122.95-124.93	1.98	2	13.6	AI794821	122.63	Satt338	123.79
C2	36.90	98.42	96.2-100.63	4.43	2	5.50	R092_3	96.13	Sat_076	99.18
D1a	28.99	57.45	56.53-58.36	1.83	3	8.56	Satt254	56.40	Satt203	59.00
D1a	28.99	70.74	68.87-72.62	3.75	2	9.10	Satt198	68.62	Satt439	72.30
D2	22.25	77.41	75.24-79.58	4.34	3	10.17	Sat_292	75.29	Satt461	80.20
E	22.24	26.14	23.51-28.77	5.26	2	14.35	OP_M12b	22.84	K229_1	28.30
E	22.24	32.71	29.92-35.5	5.58	2	20.50	K229_1	28.27	Satt573	35.80
F	27.42	2.16	1.29-3.02	1.73	2	12.17	M8E6mr1	1.09	Satt343	3.04
F	27.42	18.45	16.11-20.80	4.69	2	13.59	Satt252	16.08	Satt423	20.56
G	33.03	67.32	66.09-71.10	5.01	3	12.53	A073_1	68.56	Sat_143	73.40
G	33.03	95.12	94.26-95.97	1.71	4	13.27	Sct_199	94.40	Satt191	96.60
H	16.58	89.27	88.33-90.22	1.89	3	9.63	Satt142	86.49	A748_2	90.30
I	27.16	32.5	30.93-34.07	3.14	2	27.00	B214_2	30.56	A352_2	34.70
I	27.16	37.4	36.23-48.58	12.35	5	18.22	Sat_219	36.03	Sat_105	49.30
K	29.90	102	98.26-105.74	7.48	2	11.20	R	97.13	M7E8mr3	107.00
L	49.37	34.78	33.84-35.71	1.87	2	19.50	Satt497	33.71	Satt613	36.10
L	49.37	93.10	91.60-94.60	3.00	3	11.83	DUBC015	90.34	A489_1	95.40
N	17.54	73.14	69.19-77.09	7.90	2	6.57	A808_1	68.76	Sat_304	77.10
N	15.19	95.56	92.22-98.90	6.68	3	37.31	Satt257	92.56	Satt022	102.06

Table 11. Meta-analysis results of oil content QTLs

4.1.2 Meta-analysis of protein concentration QTLs

A meta-analysis was carried out on the consensus QTL sites on 23 QTL clusters (Table 12). The site on chromosome I merged nine QTL from seven populations, with flanking markers at 33.3cM and 37.0cM, a CI of 3.7cM and an R² value of 20.8%. The site on chromosome A1 merged four QTL, predicted from four populations, into a single consensus QTL. The flanking markers for this site lay at 88.83cM and 97.49cM, the CI of the QTL was 8.66cM, and its R² value was 9.4%. The site on chromosome B2 merged four QTL, predicted from two populations, into a single consensus QTL. The flanking markers for this site lay at 71.7cM and 73.22cM, the CI of the QTL was 1.52cM, and its R² value was 3.5%. The site on chromosome E merged five QTL, predicted from three populations, into a single consensus QTL. The flanking markers for this site lay at 23.5cM and 30.3cM, the CI of the QTL was 6.7cM, and its R² value was 7.4%. The site on chromosome M merged five QTL (five populations), with flanking markers at 34.2cM and 41.5cM, a CI of 7.2cM and an R² value of 12.4%. In total, twenty-three consensus QTL were detected. The confidence interval at all sites ranged from 1.52-14.31cM, and the proportion of the phenotypic variance associated with each of them from 1.5%-20.8%.

LG	AIC value	Meta-QTL Position (cM)	95% C.I. (cM)	Map distance	Original QTL number	Mean R ²	L-marker	L-marker Position (cM)	R-marker	R-marker Position (cM)
A1	15.64	93.16	88.83-97.49	8.66	4	9.40	Satt174	88.58	Sat_271	97.76
A2	39.23	147.79	142.48-153.09	10.61	2	3.10	T036_1	141.08	Satt228	154.11
B1	16.19	32.56	29.33-35.79	6.46	3	7.00	A109_1	29.17	Satt251	36.48
B2	7.98	31.16	25.86-36.46	10.60	2	14.50	Sat_342	20.31	A343_1	37.99
B2	7.98	49.65	44.35-54.95	10.60	2	6.80	B142_1	43.58	Satt168	55.20
B2	7.98	72.46	71.70-73.22	1.52	4	3.50	Satt272	71.68	DOP_F04	73.54
C1	73.46	15.69	10.39-20.99	10.60	2	9.40	SOYGPATR	10.34	A463_1	21.04
C1	73.46	63.08	57.78-68.38	10.60	2	13.70	V38a	54.19	A519_3	69.30
C1	73.46	93.85	88.55-99.15	10.60	2	11.00	Sat_207	87.31	Bng044_2	107.61
C1	73.46	123.76	119.43-128.09	8.66	3	13.20	Bng012_1	108.08	Satt164	132.46
C2	29.4	119.19	115.55-122.82	7.27	3	15.40	Satt708	115.49	A538_1	123.37
E	54.51	26.90	23.55-30.25	6.70	5	7.40	OP_M12b	22.84	B174_1	30.88
E	54.51	45.21	43.88-45.98	2.10	3	12.00	Satt268	44.27	R028_2	46.10
E	18.24	61.40	56.08-66.72	10.64	3	5.40	A226H_2	54.85	Satt553	67.92
G	43.52	67.62	62.31-72.92	10.61	2	13.80	Satt199	62.16	Sat_143	73.42
G	43.52	93.60	88.30-98.91	10.61	2	10.20	AF162283	87.94	L154_1	99.33
H	26.99	87.97	81.09-93.70	12.61	3	9.20	Satt302	81.04	A810_1	97.53
I	77.57	35.78	33.31-36.97	3.66	9	20.80	A144_1	32.42	Satt239	36.94
M	42.72	37.89	34.27-41.50	7.23	5	12.38	Satt567	33.47	DOP_H14	41.84
N	18.33	32.38	27.07-37.68	10.61	2	9.50	Satt631	26.14	Satt584	37.98
N	9.78	79.50	74.50-84.50	10.00	3	11.00	BLT015_1	74.49	Satt234	84.60
N	9.78	98.03	94.02-102.06	8.04	2	1.50	Sat_306	93.11	Satt022	102.06
O	14.12	72.10	64.95-79.26	14.31	2	7.50	Sat_282	63.81	Satt477	82.09

Table 12. Meta-analysis results of protein concentration QTL

4.1.3 Meta-analysis of Fatty acid QTLs

A meta-analysis was carried out on the consensus QTL sites on 19 QTL clusters (Table 13). Some sites were related with only one trait. The site on linkage group A1, with flanking markers Sat_137 and A487_1, a C.I. of 7.44cM was related with Palmitic Acid Content. The site on linkage group B2, with flanking markers Sat_189 and Satt556, a C.I. of 0.4cM was related with Stearic Acid Content. The site on linkage group D2, with flanking markers Satt461 and Sat_114, a C.I. of 8.66 cM was related with Olelic Acid Content. The site on linkage group N, with flanking markers Satt530 and Satt683, a C.I. of 3.34cM was related with Linoleic Acid Content. The site on linkage group E, with flanking markers OP_M12b and A636_1, a C.I. of 3.09cM was related with Linolenic Acid Content. However, several sites were related with at least two traits. The site on linkage group C2, with flanking markers Sat_312 and Satt319, a C.I. of 10.6cM was related with Olelic Acid Content and Palmitic Acid Content. The site on linkage group D2, with flanking markers L026_1 and Satt615, a C.I. of 0.38cM was related with Linoleic Acid Content and Olelic Acid Content. The site on linkage group G, with flanking markers K493_1 and T005_2, a C.I. of 6.12cM was related with Olelic Acid Content, Pamitic Acid Content, and Stearic Acid Content.

Trait	LG	AIC value	Meta-QTL position(cM)	95% C.I. (cM)	Map distance	L-marker	R-marker
Pal	A1	64.01	3.54	0-7.44	7.44	Sat_137	A487_1
Pal	A1	64.01	15.76	10.46-21.07	10.61	Satt572	Satt276
Ole	A1	64.01	92.41	89.06-95.77	6.71	A104_1	A170_1
St	B2	60.00	73	72.8-73.2	0.4	Sat_189	Satt556
Lio	B2	60.00	90.49	86.19-94.78	8.59	AW620774	A741_1
Ole,Pal	C2	11.04	113.39	108.09-118.69	10.6	Sat_312	Satt319
Pal	D1b	28.81	73.12	70.57-75.67	5.10	Satt141	Satt290
Ole	D2	34.21	83.00	78.67-87.33	8.66	Satt461	Sat_114
Lin,Ole	D2	34.21	91.00	90.81-91.19	0.38	L026_1	Satt615
Lio	E	35.08	25.38	23.84-26.93	3.09	OP_M12b	A636_1
Lio,Ole	E	35.08	45.09	41.34-48.84	7.50	Satt483	Satt452
Ole,Lin	G	127.82	0.72	0-3.65	3.65	Satt163	Satt038
Ole,lin	G	127.82	21.90	16.59-27.2	10.61	Satt235	Satt130
Ole	G	127.82	49.25	45.5-53	7.50	Satt131	Satt566
Ole,Pal,St	G	127.82	80.67	77.61-83.73	6.12	K493_1	T005_2
Lin,Lio	K	11.08	42.89	37.58-48.19	10.61	Satt555	Sct_196
Ole	L	69.71	31.89	27.56-36.22	8.66	Sat_397	Sat_191
Ole	L	69.71	66.11	62.36-69.86	7.50	gy3E_1	Satt166
Lin	N	6.69	34.09	32.42-35.76	3.34	Satt530	Satt683

Note: Pal, St, Ole, Lin, Lio were the abbreviation of Palmitic acid, Stearic acid, Oleic acid, Linoleic acid, and Linolenic acid, individually.

Table 13. Meta-analysis results of of fatty acid QTLs

4.1.4 Meta-analysis of amino acid content QTLs

A meta-analysis was carried out on the consensus QTL sites on 26 QTL clusters (Table 14). Most sites were related with more than two kind of amino acid content. The site on linkage group A1, with flanking markers Sat_344 and Sat_410 at 19.38cM and 29.63cM, a C.I. of 8.66cM was an admixture related with Glycine, Threonine, and Alanine content. The site with the minimal confidence interval on linkage group L, with flanking markers Satt495 and Sat_408 at 0.00 cM and 1.31cM, a C.I. of 1.86cM was related with Alanine, Glycine, Serine, Threonine, and Phenylalanine content. However, the site on linkage group M, with flanking markers GMSC514 and Satt201 at 3.05cM and 13.56cM, a C.I. of 8.66cM was mainly related with Methionine content.

LG	AIC value	Meta-QTL position(cM)	95% C.I. (cM)	Map distance	L-marker	L-marker Position (cM)	R-marker	R-marker Position (cM)
A1	23.69	25.56	21.23-29.89	8.66	Sat_344	19.38	Sat_410	29.63
A2	47.19	36.77	32.44-41.10	8.66	Satt589	33.96	Satt315	45.29
A2	47.19	107.05	102.72-111.38	8.66	Satt233	100.09	Sct_194	113.57
B2	24.61	55.2	51.45-58.95	7.50	Sct_034	51.45	Satt416	56.96
C1	11.04	74.46	69.16-79.76	10.60	Satt607	67.03	Satt476	80.62
D1a	47.19	59	55.65-62.35	6.70	Satt515	55.68	Satt580	62.37
D1b	53.30	75.67	70.37-80.97	10.60	Sat_135	70.65	Satt644	79.42
D1b	53.30	116.35	113.52-119.18	5.66	Sat_183	112.63	Sat_198	118.95
D2	47.37	47.73	42.43-53.03	10.6	Satt372	39.35	Satt582	53.85
D2	47.37	92.12	89.06-95.18	6.12	Satt488	89.20	Satt301	93.71
E	11.04	44.76	39.46-50.06	10.60	Sat_136	39.16	Sat_273	47.50
F	38.17	16.08	13.43-18.73	5.30	Satt269	11.37	Satt149	18.13
G	62.32	16.4	13.05-19.75	6.7	Satt570	12.74	Satt235	21.89
G	62.32	54.51	50.76-58.26	7.50	Satt303	53.42	Sat_088	58.00
I	11.04	82.78	77.48-88.08	10.60	Satt330	77.84	Satt623	92.52
J	23.69	11.74	6.44-17.04	10.60	AW310961	5.19	Satt674	15.95
J	23.69	43.01	37.71-48.31	10.60	Sat_370	37.40	Sat_366	52.84
K	40.45	30.28	25.95-34.61	8.66	Satt102	30.28	Satt137	36.99
K	40.45	46.63	41.33-51.93	10.60	Satt178	40.86	Sat_116	52.28
L	103.86	0.00	0.00-1.86	1.86	Satt495	0.00	Sat_408	1.31
L	103.86	31.72	29.22-34.22	5.00	Sat_405	29.62	Satt313	34.54
L	103.86	61.35	56.05-66.65	10.6	Satt156	56.14	Satt166	66.51
M	101.13	7.84	3.51-12.17	8.66	GMSC514	3.05	Satt201	13.56
M	101.13	33.47	29.14-37.80	8.66	Satt567	33.47	Satt435	38.94
M	101.13	73.37	70.87-75.87	5.00	Satt494	71.71	Sat_288	76.41
O	35.53	13.60	10.25-16.95	6.70	Satt487	9.53	Satt492	17.25

Table 14. Meta-analysis results of amino acid content QTLs

4.1.5 Meta-analysis of isoflavone content QTLs

A meta-analysis was carried out on the consensus QTL sites on 10 QTL clusters (Table 15). Although there were five sub-component of isoflavone content. Most sites were related with more than only one kind among them. The site on linkage group A1, with flanking markers Sat_368 and Satt165 at 10.60cM and 14.37cM, a C.I. of 10.60cM was related with daidyzin content. The three sites on linkage group B1, with flanking left markers Sat_261, Satt 197, and Sct_026 at 32.95 cM, 46.39, and 78.13cM, corresponding right markers Satt638, Sat_247, and Satt444 at 37.80cM, 49.73cM, and 85.92cM, the C.I. of 6.12cM, 6.12cM, and 7.55cM were all related with Gly content.

LG	AIC value	Meta-QTL position(cM)	95% C.I. (cM)	Map distance	L-marker	L-marker Position (cM)	R-marker	R-marker Position (cM)
A1	11.04	17.16	11.86-22.46	10.60	Sat_368	14.37	Satt165	23.00
B1	109.03	36.48	33.42-39.54	6.12	Sat_261	32.95	Satt638	37.80
B1	109.03	46.39	43.33-49.45	6.12	Satt197	46.39	Sat_247	49.73
B1	109.03	81.7	77.90-85.45	7.55	Sct_026	78.13	Satt444	85.92
B2	11.04	93.49	88.19-98.79	10.60	Satt534	87.59	Satt560	97.92
H	15.57	81.04	76.71-85.37	8.66	Sat_158	73.46	Satt637	85.79
K	40.51	41.52	36.21-46.82	10.61	Satt055	32.96	Satt727	46.80
K	40.51	52.28	47.95-56.61	8.66	Satt337	47.38	Satt273	56.62
N	29.61	45.14	39.84-50.44	10.60	Sat_208	39.35	Satt387	53.25
N	29.61	74.99	70.66-79.32	8.66	Satt549	53.25	Sat_091	79.51

Table 15. Meta-analysis results of isoflavone content QTLs

4.2 Meta-analysis results of biotic stress resistance QTLs

4.2.1 Meta-analysis of fungal disease resistance QTLs

A meta-analysis was carried out on the consensus QTL sites on 23 QTL clusters (Table 16). In total, 9 kind of soybean fungal disease-resistance QTLs were integrated. For brown stem rot, in short BSR, one site was the most notable cluster of integrating 14 former researches with flanking markers Sctt011 and Satt547 at 62.88cM and 67.79cM on linkage group J, a C.I. of 3.78cM. For phytophthora root rot, in short phytoph, one site was on linkage group F with flanking markers Satt252 and Satt149 at 16.08cM and 18.12cM, a C.I. of 0.84cM. Another was on linkage group J with flanking markers Satt414 and Satt596 at 37.04cM and 39.64cM, a C.I. of 1.82cM. For sclerotinia stem rot, in short Sclero, the former research results were more dispersed. one main site was on linkage group E with flanking markers Satt720 and A517_1 at 20.80cM and 26.02cM, a C.I. of 4.52cM. Another was on linkage group O with flanking markers Satt243 and Sat_190 at 119.50cM and 129.80cM, a C.I. of 8.66cM. For sudden death syndrome, in short SDS, one main site was on linkage group D2 with flanking markers Satt662 and Sat_001 at 87.88cM and 92.12cM, a C.I. of 4.11cM. Another was on linkage group G with flanking markers Satt163 and B053_1 at 0.00cM and 5.77cM, a C.I. of 4.21cM. Other results for remain diseases were listed in table and above Fig. 6.

LG	AIC value	Meta-QTL position(cM)	95% C.I. (cM)	Map distance	L-marker	L-marker Position (cM)	R-marker	R-marker Position (cM)
A2	24.04	36.77	31.47-42.07	10.60	Satt480	28.44	Satt315	45.29
A2	24.04	106.72	102.46-110.98	8.52	Satt233	100.09	Satt329	110.94
C2	26.31	40.30	35.00-45.60	10.60	Sat_062	30.80	Satt291	45.76
C2	26.31	115.47	111.23-119.70	8.47	Satt365	111.68	Staga001	119.85
D2	53.21	81.29	77.54-85.04	7.50	Sat_222	76.69	Satt226	85.15
D2	53.21	90.04	87.98-92.09	4.11	Satt662	87.88	Sat_001	92.12
E	13.94	23.85	21.59-26.11	4.52	Satt720	20.80	A517_1	26.02
F	32.21	16.91	16.49-17.33	0.84	Satt252	16.08	Satt149	18.12
F	32.21	19.21	17.99-20.43	2.44	Satt252	16.08	Satt423	20.56
F	32.21	84.17	78.87-89.47	10.6	Satt334	78.06	Sat_313	91.87
G	117.8	3.87	1.77-5.98	4.21	Satt163	0.00	B053_1	5.77
G	117.8	46.80	43.31-50.29	6.98	Sat_308	43.09	Satt352	50.53
G	117.8	83.00	78.20-87.79	9.59	A121_2	78.05	AF162283	87.94
G	117.8	95.70	90.40-101.01	10.61	A245_2	89.97	Sat_117	100.00
J	139.2	38.36	37.45-39.27	1.82	Satt414	37.04	Satt596	39.64
J	139.2	49.98	46.98-52.98	6.00	Sat_093	46.09	Sat_366	52.84
J	139.2	65.66	63.77-67.55	3.78	Sc tt011	62.88	Satt547	67.79
K	13.94	80.43	73.15-87.71	14.56	Satt499	71.00	A841_1	87.04
L	19.65	30.93	26.02-35.85	9.83	Satt388	23.55	Satt613	36.05
M	25.49	54.83	51.08-58.58	7.50	Satt463	50.10	Satt626	58.60
N	15.83	42.15	41.40-42.91	1.51	Sat_275	40.81	Sat_280	43.45
O	43.87	84.99	79.77-90.21	10.44	A878_1	78.33	Bng070_1	89.98
O	43.87	125.43	121.10-129.76	8.66	Satt243	119.50	Sat_190	129.80

Table 16. Meta-analysis results of fungal disease resistance QTLs

4.2.2 Meta-analysis of insect-resistance QTLs

A meta-analysis was carried out on the consensus QTL sites on 14 QTL clusters (Table 17). The QTL intervals were reduced from 15 cM to 3.67 cM in average. For single insect-resistance, only the sites of soybean aphid-resistance and corn earworm-resistance got the meta-analysis results. 3 true QTLs were related with soybean aphid resistance. Two sites were on linkage group F, with flanking left markers j11_1 and R045_1 at 7.31 cM and 70.12cM, corresponding right markers BLT030_1 and Satt510 at 8.67cM and 71.41cM, the C.I. of 4.68cM and 2.37cM. The other was on linkage group M with flanking markers DOP_H14 and A131_1 at 41.84cM and 47.12cM, a C.I. of 4.07cM. 9 true QTLs were related with corn earworm resistance. One site was on linkage group D1a with flanking markers Sat_353 and R013_2 at 36.23cM and 38.09cM, a C.I. of 6.02cM. Another was on linkage group G with flanking markers Satt472 and Satt191 at 94.84cM and 96.57cM, a C.I. of 1.22cM. Others were shown in the Table 17.

Most QTLs were related with mutiple insect-resistance(Table 18). For example, The site on linkage group E, with flanking markers A135_3 and Satt575 at 0.06cM and 3.30cM, a C.I. of 3.11cM was related with corn earworm resistance and common cutworm.

Trait	LG	AIC value	Meta-QTL position(c M)	95% C.I. (cM)	Map distance	L-marker	L-marker Position (cM)	R-marker	R-marker Position (cM)
Soybean aphid	F	30.07	7.56	5.22-9.90	4.68	j11_1	7.31	BLT030_1	8.67
Soybean aphid	F	30.07	71.09	69.90-72.27	2.37	R045_1	70.12	Satt510	71.41
Soybean aphid	M	34.20	43.85	41.82-45.89	4.07	DOP_H14	41.84	A131_1	47.12
CEW	D1a	15.8	38.08	35.07-41.09	6.02	Sat_353	36.23	R013_2	38.09
CEW	D2	10.64	100.12	95.33-104.92	9.59	GMHSP179	99.04	Satt186	105.45
CEW	E	48.13	2.14	0.59-3.70	3.11	A135_3	0.06	Satt575	3.30
CEW	G	8.77	95.71	95.10-96.32	1.22	Satt472	94.84	Satt191	96.57
CEW	H	145.95	38.53	35.69-41.37	5.68	A036_1	34.29	Sc tt009	38.89
CEW	H	145.95	57.34	54.52-60.16	5.64	A130_1	56.18	Satt469	58.91
CEW	H	145.95	77.32	75.9-78.74	2.84	Sat_158	73.46	K327_1	77.53
CEW	M	31.68	56.69	55.28-58.11	2.83	Satt220	56.29	A584_3	58.50
CEW	M	31.68	60.75	60.46-61.03	0.57	Sat_258	60.47	Satt702	61.04

Table 17. Meta-analysis results of single insect-resistance QTLs

LG	AIC value	Meta-QTL position(cM)	95% C.I. (cM)	Map distance	L-marker	L-marker Position (cM)	R-marker	R-marker Position (cM)
D1a	25.01	38.08	35.07-41.09	6.02	Sat_353	36.23	R013_2	38.09
D2	10.64	100.12	95.33-104.92	9.59	GMHSP179	99.04	Satt186	105.45
E	48.13	2.14	0.59-3.70	3.11	A135_3	0.06	Satt575	3.30
F	50.58	7.56	5.22-9.90	4.68	j11_1	7.31	BLT030_1	8.67
F	50.58	71.03	69.84-72.22	2.38	R045_1	70.12	Satt510	71.41
G	22.76	95.71	95.27-96.14	0.87	Satt472	94.84	Satt191	96.57
H	235.12	35.04	32.39-37.69	5.30	A036_1	34.29	Sc tt009	38.89
H	235.12	57.56	55.65-59.48	3.83	A130_1	56.18	Satt469	58.91
H	235.12	68.96	68.07-69.84	1.77	Satt676	68.86	Satt314	69.12
H	235.12	81.57	79.75-83.40	3.65	Satt302	81.04	Sat_175	83.19
M	124.22	42.75	40.85-44.64	3.79	DOP_H14	41.84	A131_1	47.12
M	124.22	56.70	55.74-57.66	1.92	Satt220	56.29	A584_3	58.50
M	124.22	60.74	60.54-60.94	0.4	Sat_258	60.47	Satt702	61.04
N	7.28	25.60	23.53-27.66	4.13	BLT004_1	25.49	Satt631	26.14

Table 18. Meta-analysis results of multiple insect-resistance QTLs

4.2.3 Meta-analysis of soybean cyst nematode resistance QTLs

A meta-analysis was carried out on the consensus QTL sites on 16 QTL clusters (Table 19). 3 true QTLs were related with SCN race1 resistance. The main site was on linkage group G, with flanking markers H3_c6_2 and Satt309 at 2.77 cM and 4.53cM, the C.I. of 1.48cM. One true QTL was simultaneously related with SCN race2 resistance and SCN race5 resistance on linkage group B1 with flanking markers R244_1 and AQ851479 at 115.75cM and 128.66cM, a C.I. of 12.29cM. 7 true QTLs were related with SCN race3 resistance. The main site was on linkage group G with flanking markers Satt309 and B053_1 at 4.53cM and 5.77cM, a C.I. of 1.01cM. 3 true QTLs were related with SCN race4 resistance. The main site was on linkage group A2, with flanking markers Sat_162 and A486_1 at 51.86 cM and 53.16cM, the C.I. of 0.86cM. One true QTL was related with SCN race14 resistance on linkage group D2 with flanking markers Satt528 and i6_2 at 86.34cM and 93.92cM, a C.I. of 7.50cM.

Trait	LG	AIC value	Meta-QTL position(cM)	95% C.I. (cM)	Map distance	L-marker	L-marker Position (cM)	R-marker	R-marker Position (cM)
Race1	B1	11.72	94.66	89.08-100.24	11.16	Satt444	85.92	Sat_123	100.88
Race1	B2	27.24	57.89	54.52-61.26	6.74	A018_1	53.54	A329_1	62.74
Race1	G	51.3	3.79	3.05-4.53	1.48	H3_c6_2	2.77	Satt309	4.53
Race2	B1	19.81	121.68	115.53-127.82	12.29	R244_1	115.75	AQ851479	128.66
Race3	A2	53.68	58.43	55.58-61.28	5.70	Satt187	54.92	A975_2	61.29
Race3	E	103.64	38.31	36.47-40.15	3.68	Satt573	35.79	A386_1	39.98
Race3	G	334.49	5.11	4.61-5.62	1.01	Satt309	4.53	B053_1	5.77
Race3	G	334.49	30.91	27.88-33.94	6.06	Sat_315	27.48	Sat_403	34.87
Race3	G	334.49	72.98	70.13-75.84	5.71	Satt517	69.87	Satt288	76.77
Race3	G	334.49	94.8	91.45-98.15	6.70	A245_2	89.97	H3_54HE_1	98.52
Race3	J	20.29	74.00	69.67-78.33	8.66	Sat_396	69.30	Satt431	78.57
Race4	A2	9.90	52.30	51.87-52.73	0.86	Sat_162	51.86	A486_1	53.16
Race4	G	12.36	3.87	3.20-4.53	1.33	H3_c6_2	2.77	Satt309	4.53
Race4	H	18.30	59.33	54.13-64.53	10.40	Satt541	53.35	Satt052	64.10
Race5	B1	27.13	121.68	115.53-127.82	12.29	R244_1	115.75	AQ851479	128.66
Race14	D2	22.17	90.20	86.45-93.95	7.50	Satt528	86.34	i6_2	93.92

Table 19. Meta-analysis results of resistance QTLs to soybean cyst nematode

4.3 Meta-analysis results of yield QTLs

4.3.1 Meta-analysis of 100-seed weight QTLs

A meta-analysis was carried out on the consensus QTL sites on 10 QTL clusters (Table 20). All the sites were dispersed on 9 linkage groups, only 2 clusters were found on LG B2. The site with the minimal confidence interval was on linkage group D2, with flanking markers Satt458 and Satt135 at 24.52 cM and 26.05cM, the C.I. of 1.52cM.

4.3.2 Meta-analysis of lodging QTLs

A meta-analysis was carried out on the consensus QTL sites on 11 QTL clusters (Table 21). 5 clusters were found on LG L with the interval of 1.31-6.19cM, 7.85-14.03cM, 30.58-34.14cM,

36.70-41.00cM, and 92.66-111.07cM, the C.I. were 3.55cM, 3.82cM, 3.12cM, 2.78cM, and 17.04cM, individually. The site with the minimal confidence interval was on LG G, with flanking markers Sat_372 and L120_1 at 107.75 cM and 110.45cM, the C.I. was 1.73cM.

LG	AIC value	Meta-QTL position(cM)	95% C.I. (cM)	Map distance	L-marker	L-marker Position (cM)	R-marker	R-marker Position (cM)
B1	27.34	40.85	36.88-44.83	7.95	Satt251	36.48	Satt197	46.39
B2	31.71	50.36	48.53-52.19	3.66	B142_1	43.58	A108_1	53.54
B2	31.71	65.56	60.26-70.86	10.6	BLT049_2	59.82	G214_4	70.88
C2	16.89	110.19	108.64-111.75	3.11	Satt277	107.59	Satt557	112.19
D2	6.52	25.28	24.52-26.04	1.52	Satt458	24.52	Satt135	26.05
H	16.28	50.72	47.23-54.22	6.99	Satt442	46.95	A404T_3	55.39
I	33.65	55.1	52.27-57.93	5.66	A955_1	51.99	Satt049	58.82
K	14.51	15.68	14.33-17.04	2.71	Satt242	14.35	Sat_119	17.11
M	8.80	9.28	6.25-12.31	6.06	Satt636	5.00	Satt201	13.56
O	14.37	40.19	38.71-41.67	2.96	Satt653	38.10	Satt347	42.30

Table 20. Meta-analysis results of 100-seed weight QTLs

LG	AIC value	Meta-QTL position(cM)	95% C.I. (cM)	Map distance	L-marker	L-marker Position (cM)	R-marker	R-marker Position (cM)
B1	28.82	73.73	66.97-80.49	13.52	BLT043-1	66.77	Satt332	80.89
C2	29.46	112.02	110.63-113.4	2.77	Bng164-1	110.14	Satt319	113.42
C2	29.46	114.1	112.71-115.49	2.78	Satt289	112.35	A397_1	116.72
F	24.04	17.5	3.50-26.6	23.1	Satt193	3.42	Satt659	26.71
F	24.04	38.9	34.90-43.70	8.80	Satt160	33.19	Satt516	44.42
G	9.99	109.86	108.47-110.20	1.73	Sat_372	107.75	L120_1	110.45
L	26.02	4.06	2.29-5.84	3.55	Sat_408	1.31	Sle3_4s	6.19
L	26.02	10.23	8.32-12.14	3.82	BLT010_2	7.85	Satt182	14.03
L	23.53	32.22	30.66-33.78	3.12	Satt398	30.58	G214_1	34.14
L	23.53	38.16	36.77-39.55	2.78	A023_1	36.70	Satt462	41.00
L	13.09	101.7	93.18-110.22	17.04	Satt664	92.66	A802_2	111.07

Table 21. Meta-analysis results of lodging QTLs

4.3.3 Meta-analysis of soybean height QTLs

A meta-analysis was carried out on the consensus QTL sites on 12 QTL clusters (Table 22). On LG B1 and LG K, 3 clusters were found, individually. The site with the minimal confidence interval was on LG K, with flanking markers Satt441 and Satt552 at 41.00 cM and 46.00cM, the C.I. was 0.24cM.

LG	AIC value	Meta-QTL position(cM)	95% C.I. (cM)	Map distance	L-marker	L-marker Position (cM)	R-marker	R-marker Position (cM)
B1	105.37	32.61	30.75-34.47	3.72	Satt426	28.00	Sat_156	35.00
B1	105.37	56.42	54.25-58.58	4.33	Sat_149	54.00	Satt298	65.00
B1	105.37	87.44	81.87-93.01	11.14	Sat_095	81.00	Satt665	96.00
C2	18.04	105.05	102.33-107.78	5.45	Satt665	102.00	Satt365	112.00
D1a	16.92	49.04	48.20-49.88	1.68	Satt342	48.00	Sat_159	50.00
F	27.28	111.34	105.70-116.98	11.28	Sat_197	104.00	Satt218	118.00
G	21.53	10.08	4.12-16.04	11.92	Sat_168	3.90	Satt217	18.00
K	19.30	38.93	36.99-40.86	3.87	Satt137	37.00	Satt178	41.00
K	19.30	41.65	40.89-42.41	1.52	Satt178	41.00	Satt555	43.00
K	19.30	46.32	46.20-46.44	0.24	Satt441	41.00	Satt552	46.00
M	32.35	18.58	11.08-26.08	15.00	Satt590	7.80	Satt567	33.00
M	32.35	42.47	37.06-47.88	10.82	Satt540	34.00	Sat_244	49.00

Table 22. Meta-analysis results of soybean height QTLs

4.4 Meta-analysis of soybean growth stage QTLs

A meta-analysis was carried out on the consensus QTL sites on 7 QTL clusters for R1 period (Table 23), 2 QTL clusters for R8 period(Table 24), and 10 QTL clusters for multiple period(Table 25). Three main sites related with R1 period were on linkage group J, with flanking left markers Satt076, A461_1, and K385_1 at 61.40cM, 87.90cM and 101.30cM, corresponding right markers L050_8, Bng095_1, and Sat_245 at 72.70cM, 100.40cM, and 115.10cM, the C.I. were 10.61cM, 8.66cM, and 10.60cM. The site with the minimal confidence interval was on LG C2, with flanking markers Satt365 and Satt658 at 111.70 cM and 113.60cM, the C.I. was 1.63cM.

One site related with R8 period was on LG C2, with flanking markers A397_1 and Sat_263 at 116.70 cM and 118.80cM, the C.I. was 0.90cM. The other site related with R8 period was on LG L, with flanking markers Satt156 and Satt678 at 56.10 cM and 70.20cM, the C.I. was 9.64cM.

LG	AIC value	Meta-QTL position(cM)	95% C.I. (cM)	Map distance	L-marker	L-marker Position (cM)	R-marker	R-marker Position (cM)
C2	24.64	106.39	98.1-107.62	9.52	Satt363	98.10	Satt277	107.60
C2	24.64	112.75	111.98-113.61	1.63	Satt365	111.70	Satt658	113.60
M	20.03	33.48	32.48-34.47	1.99	Ts	30.20	Satt540	35.80
M	20.23	18.58	11.08-26.08	15.00	Satt590	7.80	Mng339_1	27.30
L	47.46	67.38	62.08-72.69	10.61	Satt076	61.40	L050_8	72.70
L	47.46	93.26	88.93-97.59	8.66	A461_1	87.90	Bng095_1	100.40
L	47.46	107.24	101.94-112.54	10.60	K385_1	101.30	Sat_245	115.10

Table 23. Meta-analysis results of R1 period QTLs

For multiple periods, some sites were only related with reproductive periods, such as Mul1, Mul2, Mul3, Mul4, Mul9, and Mul10; some site were only related with vegetative periods, such as Mul5 and Mul6; some site were related with both reproductive periods and vegetative periods. Mul3 was very special for its long-term effect on the six of eight reproductive periods.

L G	AIC value	Meta-QTL position(cM)	95% C.I. (cM)	Map distance	L-marker	L-marker Position(cM)	R-marker	R-marker Position(cM)
C2	28.03	117.66	117.21-118.11	0.90	A397_1	116.70	Sat_263	118.80
L	16.87	64.19	59.37-69.01	9.64	Satt156	56.10	Satt678	70.20

Table 24. Meta-analysis results of R8 period QTLs

Locus name	LG	Position(cM)	Flanking Marker	Period
Mul1	C1	105.06	Sat_076-K011_3	R1, R7
Mul2	C1	112.43	Satt365-Satt658	R1, R8
Mul3	D1a	55.89	Satt515-Sat_201	R1, R2, R3, R4, R5, R7
Mul4	D1a	63.76	Satt343-Satt507	R2, R4, R6, R8
Mul5	D1b	67.09	A605_1-Sat_423	V8, V9
Mul6	D1b	73.41	Satt290	V11, V12
Mul7	D1b	78.02	Bng047_1-Sat_169	V13, V14, R3, R4, R5
Mul8	D1b	80.84	Satt644-Satt041	V18, R1, R3
Mul9	F	26.98	Satt659-Satt206	R1, R3, R7
Mul10	J	43.01	Satt380	R1, R3, R7

Table 25. Meta-analysis results of multiple period QTLs

5. Discussion

Soymap2, the reference map

A new public map, soymap2, was constructed by Song (2004). Five soybean genetic maps, including molecular genetic maps of two F2 populations, A81-356022 × PI468916 and Clark × Harosoy, and three RIL populations, Minsoy × Noir1, Minsoy × Archer, and RILs of Noir 1 × Archer, were integrated. The public map contains 20 LGs and 1,849 markers, including 709 restriction fragment length polymorphism (RFLP) markers, 1,015 Simple Sequence Repeat (SSR) markers, 73 random amplified polymorphic DNA (RAPD) markers, six amplified fragment length polymorphism (AFLP) markers, and 46 markers of other types. This integrated map shows a very high density of SSR and RFLP markers, commonly used to map QTLs. Thus, QTLs from these maps could be easily projected onto the public map.

Using of meta-analysis in MAS

MAS is an important strategy for crop improvement. Recently, MAS has been successfully used to increase the quality and yield of wheat (Romagosa. 1999) and rice (Wang. 2004). However, due to its validity, cost, and the low number of markers, MAS has not been widely applied in crops. The accuracy of mapping QTLs decides the efficiency of gene discovery and cloning.

Meta-analysis is an important tool in linkage analysis, optimize QTL, shrink the confidence interval, and improve the accuracy and validity of QTL position (Löffler, 2009), and is of

particular relevance for the validation of known QTL. QTL location is affected by many factors, including genetic background, population size and analytical method, so a single study can only be taken as suggestive, unless it is based on a large enough set of experiments. Where the CI is large, it is difficult to distinguish between the presence of a single locus and the presence of two (or more) loci. The meta-analysis approach, as developed by Goffinet and Gerber (2000), however does provide a means to alleviate the extent of this uncertainty, since it improves the capacity to identify the true number of QTL present, and the precision of their location by reducing their associated CI. QTL associated with early maturity in bread wheat have recently been identified using a meta-analysis-based approach (Hanocq, 2007), and similarly, resistance to gray leaf spot in maize has been genetically defined by the integration of >50 QTL (Shi, 2007). The proportion of the phenotypic variance explained by a given QTL (its R^2 value) is the most important parameter in deciding whether marker assistance can be more efficient than conventional phenotypic selection alone (Bernardo 2001; Bernardo and Charcosset 2006).

The molecular markers in the consensus QTL could be used for individual selection in the original mapping population. In addition, some important intervals could be enhanced by backcrossing for QTL fine mapping. However, some key aspects of MAS still require improvement. The first is how to evaluate the contribution ratio of the allele for a special locus. For some populations, the allele is major, but for others it is minor. The second aspect is how to build a practical model for MAS or molecular design, which is important for the application of markers. We hope that the meta-analysis reported here will guide the choice of QTL targeted for marker assisted selection, and it was the foundation for the process of acquiring QTL-related genes in soybean.

Use of bioinformatics tools in mining candidate genes

With the advent of soybean genomic information and bioinformatics tools, finding consensus QTL intervals in the corresponding physical map is easier, particularly for mining candidate genes (Lv et al. 2008). Bioinformatics tools are important in the process leading from QTL to the quantitative trait gene, or QTG. Wang and Paigen (2002) found that 18 of the 22 human high-density lipoprotein-cholesterol (HDL-C) QTLs were within the murine HDL-C QTLs, suggesting that murine QTLs for HDL-C levels may have homologous locations in humans and that their underlying genes may be appropriate for testing in humans. GENSCAN is a general-purpose gene identification program that analyzes genomic DNA sequences from a variety of organisms, including humans, other vertebrates, invertebrates, and plants. The InterProScan server analyzes sequences (cDNA, protein) with respect to international GO terms. In this study, traditional QTLs were integrated, and some important genes related to the important agronomic traits could be mined in the future.

6. Conclusion

In this chapter, the QTLs of 12 important agronomic traits in soybean were integrated by meta-analysis. For seed quality traits, 25 consensus QTLs of oil content were extracted from 130 initial research QTLs, 23 consensus QTLs of protein concentration from 107 QTLs, 23 consensus QTLs of fatty acid from 83 QTLs, 111 consensus QTLs of amino acid content from 111 QTLs, 10 consensus QTLs of isoflavone content from 70 QTLs. For biotic stress resistance traits, 23 consensus QTLs of fungal disease resistance were extracted from 107 initial research QTLs, 14 consensus QTLs of insect resistance from 81 QTLs, 16 consensus

QTLs of soybean cyst nematode resistance from 135 QTLs. For yield trait, 6 consensus QTLs of 100-seed weight were extracted from 78 initial research QTLs, 11 consensus QTLs of lodging from 59 QTLs, 12 consensus QTLs of plant height from 93 QTLs. For soybean growth stages, 7 consensus QTLs were extracted from 98 initial research QTLs

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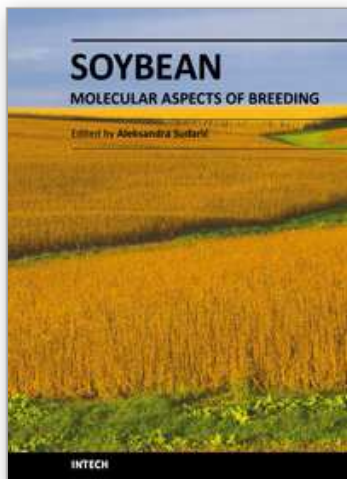
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Unit 405, Office Block, Hotel Equatorial Shanghai
No.65, Yan An Road (West), Shanghai, 200040, China
中国上海市延安西路65号上海国际贵都大饭店办公楼405单元
Phone: +86-21-62489820
Fax: +86-21-62489821

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